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Cover photo: A female orchard spider, *Leucauge venusta* (Tetragnathidae), at the center of its orb web in Estero Llano Grande State Park, Hidalgo County, Texas, USA. Photo by Bryan E. Reynolds.

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A phylogenetic classification of jumping spiders (Araneae: Salticidae)

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Abstract. The classification of jumping spiders (Salticidae) is revised to bring it into accord with recent phylogenetic work. Of the 610 recognized extant and fossil genera, 588 are placed at least to subfamily, most to tribe, based on both molecular and morphological information. The new subfamilies Onomastinae, Asemoneinae, and Eupoinae, and the new tribes Lapsiini, Tisanibini, Neonini, Mopsini, and Nannenini, are described. A new unranked clade, the Simonida, is recognized. Most other family-group taxa formerly ranked as subfamilies are given new status as tribes or subtribes. The large long-recognized clade recently called the Salticoida is ranked as a subfamily, the Salticinae, with the name Salticoida reassigned to its major subgroup (the sister group to the Amycoida). Heliophaninae Petrunkevitch and Pelleninae Petrunkevitch are considered junior synonyms of Chrysillini Simon and Harmochirina Simon respectively. Spartaeinae Wanless and Euophryini Simon are preserved despite older synonyms. The genus *Meata* Żabka is synonymized with *Gedea* Simon, and *Diagondas* Simon with *Carrhotus* Thorell. The proposed relationships indicate that a strongly ant-like body has evolved at least 12 times in salticids, and a strongly beetle-like body at least 8 times. Photographs of living specimens of all 7 subfamilies, 30 tribes, and 13 subtribes are presented.

Keywords: Phylogeny, taxonomy, systematics, biogeography

Jumping spiders, with more than 5800 species described (World Spider Catalog 2015), are familiar in all non-polar terrestrial ecosystems, and yet there has not been a new comprehensive classification of the family in more than a century. Eugène Simon's 1901–1903 landmark classification of salticids was remarkable for its breadth, covering the family's worldwide diversity. He separated the Salticidae by cheliceral dentition into three large sections (Pluridentati, Fissidentati, Unidentati), an arrangement that Simon suggested, correctly, to be somewhat artificial. His further division of the family into 69 groups is also rather artificial, because heavy reliance on basic body shape led him to group superficially similar species that we now recognize as unrelated. Petrunkevitch (1928) and Roewer (1954) substantially maintained Simon's arrangement. The next major advance was from Prószyński (1976), who used genitalic characteristics, radically reorienting salticid classification to be considerably more natural than Simon's. However, it included only a small fraction of the family's genera, and subsequent work (e.g., Maddison & Hedin 2003a; Bodner & Maddison 2012) has shown the basic form of male genitalia — the general shape of the tegulum and embolus — to be frequently convergent, holding insufficient information to resolve the family reliably. Wanless (1980c, 1981a, et seq.) brought cladistic reasoning to salticids, clarifying relationships among non-salticine salticids. Despite these advances, the relationships of most salticid genera remained unclear.

Five developments now enable a comprehensive new phylogenetic classification of the family. First, an increase in taxonomic effort during the last several decades by Prószyński, Wesołowska, Żabka, Logunov, Galiano, Wanless, Zhang, Maddison, Peng, Ruiz, Marusik, and others has made many species better known. Second, these authors, along with Edwards, Szűts, and others, have improved our phylogenetic interpretations of morphological variation. Third, the compilation of online libraries of illustrations (Prószyński 1995, 2015; Metzner 2015) has greatly facilitated inspection and comparison of morphological variation across the family, giving clues to the placement of many genera. Fourth, electronic catalogs (Platnick 2014; World Spider Catalog 2015) have assisted many aspects of this work, providing a complete list of target genera to be placed. Molecular phylogenetic studies are the fifth major development. They have approached a sufficient breadth of coverage so as to represent most of the distinctive groups of genera (Hedin & Maddison 2001; Maddison & Hedin 2003a, b; Andriamalala 2007; Su et al. 2007; Maddison et al. 2008, 2014; Bodner & Maddison 2012; Zhang & Maddison 2013, 2014; Ruiz & Maddison in press). They also have enough support that we can be confident of the basic structure of the family (Bodner & Maddison 2012; Maddison et al. 2014).

In order to generate the classification, we would ideally perform a phylogenetic analysis for all genera of salticids based on scored character data, both molecular and morphological. Such formal data are not available for most of the genera, and waiting for them would leave us without a good classification for years. However, we have a strong scaffold from the molecular phylogeny, and we can identify where most salticid genera would attach to it, based on similarities in genitalic and somatic features, even if we lack clear synapomorphies. The classification proposed here (Tables 1 and 2) is therefore based on both molecular and morphological information. It is, of course, tentative, but by placing most salticid genera into groups, it increases the chances that each will be considered further, no doubt leading to revisions in the arrangement.

METHODS

The list of genera to be placed in groups was compiled from Platnick's (2014) catalog version 15 by special modules in Mesquite 3.01 (Maddison & Maddison 2014), which allowed easy tabulation of species and geographic distribution. To this were added new genera and synonymies from some more recent papers (Wesołowska et al. 2014; Żabka 2014; Caleb et al. 2015; Dunlop et al. 2015; Patoleta & Żabka 2015; Richman 2015; Zhang & Maddison 2015; Edwards in press; Ruiz & Maddison in press). Although an attempt was made to include all described genera, a few species described after the date of Platnick (July 2014) are missing from the counts.

Counts of species currently in subtribes and tribes are given, but I did not attempt to decide for every species whether it belonged in the tribe or subtribe. Rather, the counts for a taxon are derived from the counts of species currently assigned to its contained genera. Given the state of salticid taxonomy, there are some genera that contain species properly belonging to different tribes, and so some will be misassigned in the eounts given. These species counts should therefore not be relied upon for quantitative analyses; they are intended merely to convey a sense of diversity.

Authors of family-group taxon names are given in Table 1, and of generic names in Table 2, rather than listed in the text on first use. Synonymies under each taxon include any synonyms and changes of rank, as well as the names used by Simon (1901, 1903), Petrunkevitch (1928), Roewer (1954) and Prószyński (1976).

Family-group taxa and ranking.—My goal is not to question generic limits, but to place existing genera within suprageneric taxa (subfamilies, tribes and subtribes). A few family-group taxon names for salticids were proposed in the 19th century: Attidae by Sundevall (1833), Salticidae by Blackwall (1841), Lyssomanidae by Blackwall (1877), Dendryphantidae by Menge (1879), Athamii and Simonellii by Peckham et al. (1889), and Synemosinae, Ballinae, Marptusi and Phidippi by Banks (1892). F.O. Pickard-Cambridge's Biologia Centrali Americana (section containing salticid classification published 1900) added Synageleae, Amyceae, and Homalotteae. However, one major work provided most of the names needed for our current family-group taxa: Simon's second edition of Histoire Naturelle des Araignées (1901, 1903). Simon gave the first comprehensive and detailed classification of the family, adding dozens of names for taxa through his many "groups".

Salticid classification moved from Simon's groups toward a system of taxa ranked as subfamilies beginning with Petrunkevitch (1928), who dispensed with the rank of "group", instead consolidating Simon's 69 groups to form 23 subfamilies, a few of which were new. Roewer (1954) maintained Petrunkevitch's subfamilies, but layered them over top of Simon's groups and a few new groups of his own. Prószyński (1976) and most of the subsequent literature has focused on subfamily as the primary rank for suprageneric taxa within Salticidae. Since Prószyński (1976), one subfamily has been added by each of Wanless (1984a), Bodner & Maddison (2012), Edwards (in press), and Ruiz & Maddison (in press).

In recent years, unranked taxa such as the Amycoida (Maddison & Hedin 2003a) have been established for salticid groups. This has been convenient, especially while our understanding of salticid relationships was changing rapidly. However, these unranked groups, along with the failure to place many genera into higher taxa, has left the classification in disarray, with subfamilies (such as Heliophaninae) existing alongside Simon's groups (such as Hasarieae) of unclear rank, and with many genera unplaced. Although ranks carry no biological meaning, a system of ranked taxa can be useful to provide a predefined low-resolution subset of highlighted clades for non-experts and alphabetizers. I therefore attempt to regularize salticid taxa into standard ranks.

There are two primary consequences of the review of ranking. First, most subfamilies are demoted to tribes, as per status changes indicated in Table 1. The traditional use of "subfamily" in salticids is too fine-grained, with dozens of subfamilies and little chance for a formal higher order structure. Salticid systematists may have been inclined to use such small subfamilies because of the difficulty of finding broader relationships before molecular data were available. The new classification has 7 subfamilies and 30 tribes (Table 1).

Second, the name "Salticoida", previously applied to the enormous elade of familiar salticids, will change its meaning to a stricter sense (to exelude the Amycoida) so as to permit the larger clade to be renamed as a formal subfamily, the Salticinae. Several other unranked taxa that serve to group tribes together remain within the Salticinae, including the Amycoida, Astioida, Marpissoida and Saltafresia.

The use of tribes and subtribes leads to ambiguity in the meaning of the adjectival forms "salticine", "spartaeine", "dendryphantine", "plexippine", and "aelurilline". If not otherwise specified, by default I use "salticine" to refer to the subfamily, "spartaeine" to the tribe, and the last three to the respective subtribes. For the last three, this convention most closely maintains previous use of the terms.

Phylogenetic decisions.—The broader structure of this classification is based primarily on recent molecular phylogenetic results (Fig. 1; Hedin & Maddison 2001; Maddison & Hedin 2003a; Su et al. 2007; Maddison et al. 2008, 2014; Bodner & Maddison 2012; Zhang & Maddison 2013; Ruiz & Maddison in press), as well as a few unpublished molecular results. I would not have relied so much on the molecular results were they nonsensical to the morphological patterns, but they are not. The groups discovered by molecular data have coherence in general body form, in genitalia, and in geographical distribution. However, we lack precise morphological synapomorphies to corroborate many of our groups. While such synapomorphies no doubt exist, to date we have examined too few character systems in too little detail to have found them. I have given preference to molecular data primarily because we have hundreds of molecular characters, but only a few well gathered and consistently described morphological characters.

The molecular phylogeny is merely a skeleton, as molecular data have been gathered for only about half of the genera (Table 2 marks genera for which molecular data are available). Thus, I have added flesh to the bones by attaching other genera by morphological data, with varying degrees of certainty. In some cases, clear synapomorphies link a genus to a group well placed by molecules (e.g., *Kima* and others sharing the loss of retromarginal cheliceral teeth and ant-like body with the well-placed *Leptorchestes*). In other eases, there are no documented linking traits well demonstrated to be derived, but an overwhelming resemblance in many traits establishes a placement firmly (e.g., *Simaethula* as a simaethine). Under each tribe or subtribe, if there are no molecular data or previous literature justifying the inclusion of a genus, I give some indication as to why it is placed there. In making such choices, I am reassured by our experience in gathering molecular data: in many cases we have guessed by morphology that a genus would be in a particular group even though we lacked clear synapomorphies, and the molecular data have almost always corroborated our guess.

Molecular synapomorphies are indicated for some of the new tribes and subfamilies. Insofar as these are single nucleotide site changes, they do not supply strong evidence for monophyly,

but are given for the sake of the formal diagnosis of the new taxa. No attempt was made to list such molecular synapomorphies for other taxa.

In order to assess morphological similarities and synapomorphies, besides consulting the literature, I made heavy use of Prószyński's (2015) compilation of drawings, and to a lesser extent Metzner's (2015). Not only does Prószyński's compilation bring together in one place most of the illustrations in the literature, but it also includes many illustrations of Prószyński's that are not otherwise published, including of type specimens. This resource had an important influence at every stage of this project, for every tribe and subtribe, even where not directly cited below. Without it, the current classification would have taken far longer to achieve.

Palps.—Since Prószyński's (1976) work, the male palp has been an important focus of salticid systematics. It provides convincing or potential synapomorphies for many groups: Onomastinae, Lyssomaninae, Spartaeina, Holcolaetina, Marpissoida, Ballini, Dendryphantina, Neonini, Mopsini, Chrysillini, Euophryini, Aelurillina, and Plexippini. Several axes of variation are evident: whether the embolus is movable, whether the bulb is circular, and whether the functional tegulum appears divided by a cleft. A thorough review is beyond the scope of this paper, but some distinctions used in the discussion of taxa are explained here.

"Fixed embolus" is used to refer to an embolus that is more or less immovable relative to the tegulum, being fused thereto. "Freely movable embolus", in contrast, refers to an embolus (often spiral in form) that has substantial freedom of movement relative to the tegulum, with an extensive embolic hematodocha. There is not always a clear distinction between fixed and free, as some species have a small embolic hematodocha that permits a slight bend of the embolus away from the tegulum. Several clades have both fixed- and movable-embolus palps (e.g., Amycoida, Astioida, Marpissoida, Euophryini, Aelurillini).

For fixed-embolus palps, there are two basic forms, a narrower oval form (e.g., *Hypaeus*, *Menemerus*, *Freya*, *Clynotis, Anarrhotus*, *Pellenes*, *Sitticus distinguendus* (Simon, 1868)) and a circular form (e.g., *Amycus*, *Afraflacilla*, *Chira*, *Myrmarachne*, *Epeus*, *Habronattus*, *Sitticus fasciger* (Simon, 1880)). The former typically have the embolus originating at about 9:00 to 10:00 (as on a clock face, left palp, ventral view), while the latter have the embolus arising at 8:00, or 5:00, or 2:00, or even further counterclockwise. These variants appear to be simply points along a continuum of rotation of the bulb, with the embolus getting longer and the bulb more circular as the origin of the embolus is rotated further counterclockwise. Many clades, well supported by molecular and other morphological data, separately show a diversity of rotations. Indeed, the exemplary genera noted above are respectively paired phylogenetically, with *Hypaeus* and *Amycus* both amycines, *Menemerus* and *Afraflacilla* both chrysillines, and so on. This strongly indicates considerable homoplasy in bulb rotation, and is the reason I mostly ignore the degree of rotation (embolus length), unlike Prószyński (2015), whose classification (unpublished by the rules of the ICZN 2012) appears to be heavily influenced by degree of rotation. Similar homoplasy is seen in the rotation of the spiral embolus in movable-embolus palps, where the embolus can vary from a simple curve to more than 720 degrees of spiralling (repeated in the marpissoids and many euophryine subclades).

Those fixed-embolus palps with a short embolus (i.e., bulb narrow, oval, less rotated) often have a cleft cutting diagonally from the base of the embolus across the functional tegulum, as in freyines (Galiano 1982, fig. 2) and hasariines (Logunov 1999a, fig. 24). This cleft is also seen in palps that have a movable embolus, as in dendryphantines, where the cleft forms the "tegular ledge" of Maddison (1996, fig. 3). The two regions on either side of the cleft have been named variously by authors: the more basal region (toward the subtegulum) is called the "shoulder" of the tegulum by Maddison (1996), the tegulum proper by Logunov & Cutler (1999), and the basal division of the tegulum by Edwards (in press). The region distal to the cleft (toward the embolus) is called the radix by Logunov and Cutler (1999), and the distal division of the tegulum by Edwards (in press). In more circular, rotated bulbs, this cleft is less distinct and may be absent.

CLASSIFICATION

A summary of the classification is given in Table 1, and is presented in relation to recent phylogenetic results in Fig. 1. The placement of salticid genera into subfamilies, tribes, subtribes, and unranked clades is given in Table 2, and repeated in machine-readable form in supplemental materials, online at http://dx.doi.org/10.1636/R15-55.s1. Photographs of living representatives of each of these groups are shown in Figs. 2–136.

There are four categories of genera that I leave as "*incertae sedis*". Among the extant species, some are poorly enough known that we cannot even decide whether they are salticines or not ("Salticidae *incertae sedis*", 9 genera). Others are well enough described that we know they belong to the Salticinae, but their placement is unclear, usually because we lack clear synapomorphies to place them ("Salticinae *incertae sedis*", 48 genera). The fossil genera (Dunlop et al. 2015) include some that are clearly non-salticines ("Fossil Salticidae *incertae sedis*, not in the Salticinae", 7 genera) and others poorly enough known that we cannot place them in, or exclude them from, any subfamily ("Fossil Salticidae *incertae sedis*", 6 genera). All remaining genera of salticids, 540 in total, have been placed to tribe, major clade, or subfamily.

Family Salticidae Blackwall, 1841

Sundevall, 1833: Attidae
Blackwall, 1841: Salticidae
F.O. Pickard-Cambridge, 1900: Salticidae
Simon, 1901: Salticidae
Peckham & Peckham, 1909: Attidae
Petrunkevitch, 1928: Salticidae
Roewer, 1954: Salticidae

Remarks.—See Edwards (2011) regarding the synonymy of *Attus* with *Salticus*, and thus the preference for Salticidae over Attidae.

Monophyly: Jumping spiders are united by the large anterior median eyes in the form of a long cone (Scheuring 1914; Ramírez 2014) whose retinas are vertical strips (Land 1969a; Blest et al. 1990) and by the eye arrangement: medium-sized anterior lateral eyes (ALE) just beside or behind the anterior

Table 1.—Summary of classification.

Family Salticidae Blackwall, 1841
Subfamily Onomastinae Maddison, *subfam. nov.*
Subfamily Asemoneinae Maddison, *subfam. nov.*
Subfamily Lyssomaninae Blackwall, 1877
Subfamily Spartaeinae Wanless, 1984
Tribe Spartaeini Wanless, 1984, *stat. nov.*
Subtribe Spartaeina Wanless, 1984, *stat. nov.*
Subtribe Holcolaetina Simon, 1901, *stat. nov.*
Tribe Cocalodini Simon, 1901, *stat. nov.*
Tribe Lapsiini Maddison, *trib. nov.*
Subfamily Eupoinae Maddison, *subfam. nov.*
Subfamily Hisponinae Simon, 1901
Subfamily Salticinae Blackwall, 1841
Clade Amycoida Maddison & Hedin, 2003
Tribe Gophonini Simon, 1901, *stat. nov.*
Tribe Sitticini Simon, 1901, *stat. nov.*
Tribe Bredini Ruiz & Maddison, 2015, *stat. nov.*
Tribe Scopocirini Simon, 1901, *stat. nov.*
Tribe Thiodinini Simon, 1901, *stat. nov.*
Tribe Sarindini Simon, 1901, *stat. nov.*
Tribe Simonellini Peckham, Peckham & Wheeler, 1889, *stat. nov.*
Tribe Huriini Simon, 1901, *stat. nov.*
Tribe Amycini F.O. Pickard-Cambridge, 1900, *stat. nov.*
Clade Salticoida Maddison & Hedin, 2003, new delimitation
Tribe Agoriini Simon, 1901, *stat. nov.*
Tribe Baviini Simon, 1901, *stat. nov.*
Clade Astioida Maddison, Bodner & Needham, 2008
Tribe Myrmarachnini Simon, 1901, *stat. nov.*
Tribe Neonini Maddison, *trib. nov.*
Tribe Astiini Simon, 1901, *stat. nov.*
Tribe Mopsini Maddison, *trib. nov.*
Tribe Viciriini Simon, 1901, *stat. nov.*
Subtribe Viciriina Simon, 1901, *stat. nov.*
Subtribe Simaethina Simon, 1903, *stat. nov.*
Clade Marpissoida Maddison & Hedin, 2003
Tribe Ballini Banks, 1892, *stat. nov.*
Tribe Tisanibini Maddison, *trib. nov.*
Tribe Dendryphantini Menge, 1879, *stat. nov.*
Subtribe Synagelina F.O. Pickard-Cambridge, 1900, *stat. nov.*
Subtribe Itatina Simon, 1901, *stat. nov.*
Subtribe Marpissina Simon, 1901, *stat. nov.*
Subtribe Dendryphantina Menge, 1879, *stat. nov.*
Clade Saltafresia Bodner & Maddison, 2012
Tribe Nannenini Maddison, *trib. nov.*
Tribe Hasariini Simon, 1903, *stat. nov.*
Tribe Chrysillini Simon, 1901, *stat. nov.*
Clade Simonida Maddison, *nov.*
Tribe Leptorchestini Simon, 1901, *stat. nov.*
Tribe Euophryini Simon, 1901, *stat. nov.*
Tribe Salticini Blackwall, 1841, *stat. nov.*
Tribe Aelurillini Simon, 1901, *stat. nov.*
Subtribe Aelurillina Simon, 1901, *stat. nov.*
Subtribe Freyina Edwards, 2015, *stat. nov.*
Subtribe Thiratoscirtina Bodner & Maddison, 2012, *stat. nov.*
Tribe Plexippini Simon, 1901, *stat. nov*
Subtribe Plexippina Simon, 1901, *stat. nov*
Subtribe Harmochirina Simon, 1903, *stat. nov*

median eyes (AME), behind which are the smallest eyes, behind which are the medium-sized posterior eyes. The smallest eyes, which are sometimes almost as large as the others, are here and traditionally referred to as the posterior medians (PME), although Homann (1971) argues that they are homologous to the posterior laterals of other spiders. This placement of the PMEs and posterior lateral eyes (PLE) results from a strong curvature of the posterior eye row, which can be considered another synapomorphy (Ramírez 2014). The jumping behaviour (Parry & Brown 1959; Hill 2010b), more precise than in other spiders, likely implies synapomorphies in cuticle, muscle or nervous systems, but they have not been described. Ramírez (2014) indicates several other possible synapomorphies for the family: loss of cylindrical gland spigots, gain of a median apophysis, and reversal to prograde leg orientation. Molecular data concur that the family is monophyletic (Maddison et al. 2014).

Subdivision: The basic division of the family established here, into 7 subfamilies, is based on both morphological (Wanless 1980c, 1985; Maddison 1988, 1996; Ramírez 2014) and molecular (Maddison et al. 2014) data. Table 1 presents the classification of salticids to the level of subtribe. Each of the 7 subfamilies, 30 tribes, and 13 subtribes will be considered in turn. The genera assigned to each are listed in Table 2.

With the recognition of the familiar and well-established clade as the subfamily Salticinae, the phylogeny (Fig. 1; Maddison et al. 2014) dictates that we recognize the Hisponinae and Spartaeinae as distinct subfamilies. The Eupoinae are distinctive and of unclear affiliation, and therefore provisionally separated. Most tentative is the separation of the former Lyssomaninae (Wanless 1980c) into three subfamilies, the Onomastinae, Asemoneinae, and Lyssomaninae. These three collectively have been treated as a separate family (Banks 1892; Roewer 1954) or subfamily (Galiano 1976b). They are superficially similar, sharing translucent green or yellow bodies, long legs, complex palps and the ALE placed behind and above the AME to form a second separate eye row. Their complex palps could represent a symplesiomorphy, and so do not provide evidence for their joint monophyly. Both the translucent greenish foliage-dwelling body form and displaced ALEs could be synapomorphies uniting the three groups, but alternatively they could be ancestral for the family or convergent, as other salticids show independent origins of both long-legged green body forms (e.g., *Epeus*, *Orthrus*, *Sidusa*) and displaced ALEs (e.g., *Athamas*, *Mantisatta* – see Wanless 1980c). Benjamin (2010) suggested that his morphological data support the monophyly of the former Lyssomaninae *sensu lato*, but this conclusion does not follow from his analysis, as only a single non-lyssomanine taxon was included. Wanless (1980c) suggested the Lyssomaninae *sensu lato* may be polyphletic, dividing it into three groups that correspond to the three subfamilies recognized here. Molecular analyses suggest that the Onomastinae, Asemoneinae, and Lyssomaninae may not form a clade (Maddison & Needham 2006; Su et al. 2007; Maddison et al. 2008; Bodner & Maddison 2012; Maddison et al. 2014). They are treated as separate subfamilies here, despite ambiguity in the molecular results. Even if they were to fall into a single monophyletic group, their molecular divergences are as deep as those separating other subfamilies (Maddison et al. 2014).

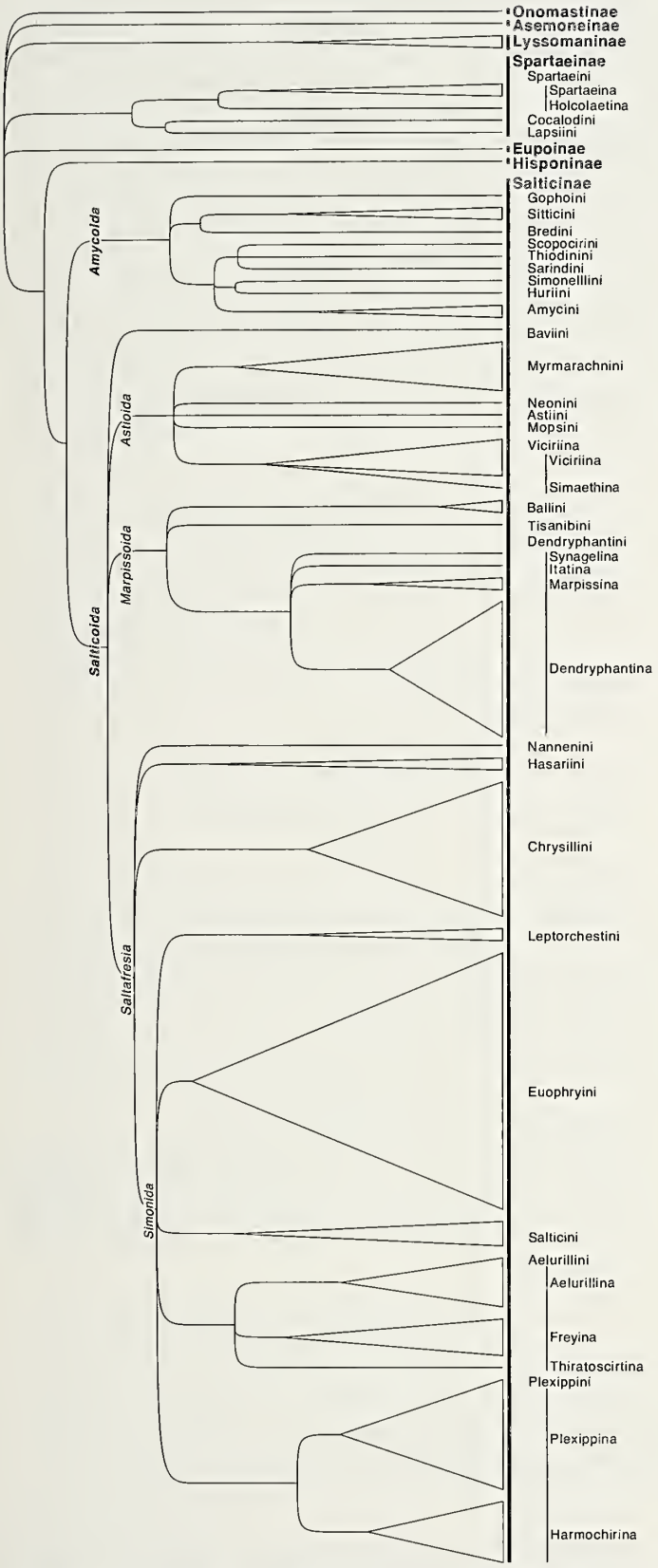


Figure 1.—Summary phylogeny of Salticidae showing higher taxa, based primarily on molecular results of Maddison et al. (2014) and others (see text). The Agoriini, somewhere within the Salticoida, is not shown. The span of each terminal clade is drawn approximately proportional to its number of described species. Divergence depths are shown approximately proportional to their inferred ages from Bodner & Maddison (2012) and Zhang & Maddison (2013), with ages not included therein interpolated subjectively using branch lengths from Maddison et al. (2014).

Putative ancestral states for salticids in various characters can be inferred from the discussions of synapomorphies under particular clades. Three worth mentioning here are the presence of a median apophysis (Maddison 2009), the presence of large posterior median eyes (Wanless 1984a), and the presence of a claw on the female palp (Maddison 1996). Relatively few salticids show these features, and those that have any one of these are instantly marked as falling outside the Salticinae.

Some Baltic Amber salticids have a characteristic constriction behind the PMEs, and hence are here considered to be hisponines. The remainder (e.g., *Eolinus*) are clearly non-salticines that cannot yet be placed to any subfamily. Although Wunderlich (2004) considered them "Coealodinae", his concept of the subfamily was paraphyletic, without synapomorphies. I therefore consider the non-hisponine Baltic salticids to be non-salticine Salticidae *incertae sedis*. While the Baltic Amber is striking for its lack of Salticinae, the younger Dominican Amber appears remarkably modern, including extant genera in such salticine groups as the euophryines and gophoines (Wunderlich 1982; Wunderlich 1988; Wolff 1990; Penney 2008).

Subfamily Onomastinae Maddison, **subfam. nov.**
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:74993737-8A80-48B6-8660-6EF149DD7A6E
(1 genus; Fig. 2)

Type genus.—*Onomastus* Simon, 1900

Remarks.—Delicate, translucent and long-legged, with highly complex palps, from the Asian tropics. As in lyssomanines and asemoneines, the ALE are above the AME, forming two separate rows. Benjamin (2010) divides *Onomastus* into two groups, a Southeast Asia clade with a broad conductor and epigynal folds, and a South Asia clade with a medial branch on the median apophysis and a TA3 tegular apophysis.

Monophyly and Diagnosis: Wanless (1980b) proposes the distinctive tegular apophysis as a synapomorphy for onomastines (Wanless 1980b, fig. 3E). Benjamin (2010) indicates two additional synapomorphies for *Onomastus* species, the absence of the retrolateral tibial apophysis (Benjamin 2010, fig. 4A) and the dorsal origin of the embolus (Benjamin 2010, figs. 9A, 15A).

Subfamily Asemoneinae Maddison, **subfam. nov.**
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:018DD4F2-4695-4E50-A287-DD8ADFC151E2
(5 genera; Figs. 3, 4)

Type genus.—*Asemonea* O. Pickard-Cambridge, 1869

Remarks.—The African and Asian asemoneines are translucent and long-legged (Wanless 1980a, c), resembling onomastines and lyssomanines. They correspond to Wanless's (1980c) "Group III" among the lyssomanines *sensu lato*. *Asemonea* is widely distributed in the African and Asian tropics. Most of the rest of the group's diversity is in Africa, with four genera occurring in Madagascar.

Monophyly and Diagnosis: This group is distinguished by the unusually medial position of the PME, distinctly closer to the midline than is the inner edge of the ALE, an apparent synapomorphy (Wanless 1980c, figs. 2D, E, F). Molecular data (Maddison et al. 2014) unite the three sampled asemoneines, *Asemonea*, *Goleba* and *Pandisus*. Logunov (2004) suggests *Hindumanes* is near *Pandisus*, sharing their minute PLE.

Subfamily Lyssomaninae Blackwall, 1877
(2 genera; Figs. 5–7)

Blackwall, 1877: Lyssomanidae
Peckham & Peckham, 1886: Lyssomaneae
Peckham, Peckham & Wheeler, 1889: Lyssomaneae, Lyssomanii
Thorell, 1895: Lyssomaninae
F.O. Pickard-Cambridge, 1900: Lyssomaneae
Simon, 1901: Lyssomaneae
Petrunkevitch, 1928: Lyssomaninae
Roewer, 1954: Lyssomanidae
Galiano, 1976b: Lyssomaninae

Remarks.—Lyssomanines are translucent and long-legged, usually green or yellow, from the American tropics (Galiano 1980, 1998; Logunov & Marusik 2003b; Logunov 2014). They dwell on foliage, especially large leaves. As in asemoneines and onomastines, the ALE are above the AME, forming a second separate row. Two genera are described, although Maddison et al.'s (2014) results suggest that *Lyssomanes* may be paraphyletic with respect to *Chinoscopus*.

Monophyly: Wanless (1980c) suggests the membranous secondary conductor as a possible synapomorphy of lyssomanines (Wanless 1980c, figs. 2G, H). Molecular data (Maddison et al. 2014) strongly support the monophyly of the group.

Subfamily Spartaeinae Wanless, 1984
(29 genera; Figs. 8–20)

Simon, 1901: Boetheae, Cocaleae, Cocalodeae, Codeteae, Cyrbeae, Holcolaeteae, Lineae
Petrunkevitch, 1928: Boethinae
Roewer, 1954: Boethinae, Boetheae, Cocaleae, Cocalodeae, Codeteae, Holcolaeteae, Lineae
Wanless, 1984a: Spartaeinae
Wunderlich, 2004: Cocalodinae

Remarks.—Wanless's Spartaeinae and his "*Cocalodes* group", along with the lapsiines, are united here in the subfamily Spartaeinae. The names used for the subfamily and its contained groups are discussed below under "Problematic names".

Monophyly: Among non-salticine salticids, the Spartaeinae lack the distinctive green or yellow translucence of the lyssomanines, onomastines and asemoneines, lack the ocular constriction on the carapace of hisponines, and lack the small shiny bodies of eupoines. In this regard, the Spartaeinae appear generalized, united only by possibly ancestral character states. Together they have no known morphological synapomorphies. It was not necessarily expected therefore that they would be monophyletic. Rodrigo & Jackson (1992) concluded that their morphological data supported the monophyly of the group (ignoring the lapsiines, of which they were unaware), but this conclusion does not follow from their analyses, because the latter included only a single taxon outside the group (*Asemonea*). Nonetheless, the molecular data (Maddison et al. 2014) clearly show that spartaeines, cocalodines and lapsiines form a clade. Similarly generalized salticids such as *Eolinus* and *Cenattus* are known from Paleogene Baltic amber, but there is no evidence to date that they are also part of this clade.

Appearing frequently in the Spartaeinae are PMEs notably larger than in the Salticinae. However, large PMEs are also seen in some asemoneines, and some Spartaeinae have small PMEs. While PME size is therefore problematical as evidence for monophyly, it can serve as an informal identification aid: all known living salticids with large PMEs that are not *Lyssomanes*-like (i.e., are not translucent and long-legged) belong to the Spartaeinae.

The subgroups of Spartaeinae are clearly defined by geographical range, if not by morphology. The Spartaeini has known synapomorphies, but the Cocalodini and Lapsiini are not distinguished by any documented morphological synapomorphies, appearing simply to be generalized salticids. In practice, they are best distinguished by molecular data or location (Lapsiini are American; Cocalodini are Australasian except for the distinctive *Depreissia*; Spartaeini are Afro-Eurasian, except for a few Australasian species).

Tribe Spartaeini Wanless, 1984

Synonymy given under subtribe Spartaeina

Remarks.—This group was first recognized by Wanless (1985) when he proposed that *Holcolaetis* and *Sonoita* — the present Holcolaetina — are closely related to what is here called the Spartaeina. Su et al. (2007)'s concept of Spartaeinae matches the tribe Spartaeini here.

Many of the Spartaeini are known to eat other spiders, to build webs, and to invade webs of other spiders (Su et al. 2007). The Spartaeini are primarily African and Asian, with a few representatives in Europe and Australasia.

Monophyly: Wanless (1985) proposes abdominal secretory organs as a synapomorphy uniting the members of this group (Wanless 1984b, figs. 16–21; Wanless 1985, fig. 12B). The molecular data (Maddison et al. 2014) strongly support their monophyly.

Subtribe Spartaeina Wanless, 1984
(16 genera; Figs. 8–13)

Simon, 1901: Boetheae, Cocaleae, Codeteae, Cyrbeae, Lineae
Petrunkevitch, 1928: Boethinae
Roewer, 1954: Boetheae, Cocaleae, Codeteae, Lineae
Wanless, 1984a: Spartaeinae

Remarks.—This is the Spartaeinae of Wanless (1984a), delimited by the presence of a tegular furrow. It is restricted to the tropics and subtropics of the Old World (Wanless 1978b, 1979, 1981b, c, 1984a, b, 1987). The best-known member is the araneophagous *Portia* (Jackson & Blest 1982; Jackson & Hallas 1986a, 1990; Jackson & Wilcox 1990, 1993;

Jackson 1992a, b, 1995; Clark & Jackson 2000; Jaekson et al. 2001, 2008b; Jackson & Nelson 2011; Cross & Jackson 2014). The habitats of Spartaeina range from tree trunks (*Phaeacius*, *Mintonia*) to foliage (*Brettus*, some *Neobrettus*) and suspended litter near the ground (*Taraxella*).

Monophyly: A furrow in the tegulum just retrolateral from the base of the embolus, running parallel to the periphery of the tegulum, delimits this group ("tegular furrow", Wanless 1984a, figs. 35A, C, E). It does not appear to be homologous with the tegular furrow of Ramírez (2014, fig. 157) or the cleft behind the tegular ledge of Maddison (1996). Loss of the median apophysis (Wanless 1984a) is a synapomorphy, but convergent with losses in salticines, hisponines and lyssomanines. In addition, the conductor is lost or extremely redueed in most, though not all (Wijesinghe 1992). The group is strongly supported by molecular data (Su et al. 2007; Maddison et al. 2014).

Subtribe Holcolaetina Simon, 1901
(2 genera; Fig. 14)

Simon, 1901: Holcolaeteae
Roewer, 1954: Holeolaeteae

Remarks.—A strictly African group notable for the prominent conductor on the palp (Wanless 1985). Unlike the Spartaeina, holcolaetines retain a distinct median apophysis. *Holcolaetis* is a large, flat bark dweller reminiscent of *Marpissa* or *Balmaceda*, but instantly recognizable as a non-saltieine by its large PMEs.

Monophyly: Wanless (1985) suggests the two genera of holcolaetines share as synapomorphies "the characteristic form of the tegulum, median apophysis and distal haematodocha in males and epigynal flanges in females". The first three of these have not been well explained as synapomorphies, but the epigynal flanges are distinctive (Wanless 1985, fig. 11J). Molecular data support their joint monophyly (Maddison et al. 2014).

Tribe Cocalodini Simon, 1901
(6 genera; Figs. 18–20)

Simon, 1901: Coealodeae
Roewer, 1954: Cocalodeae
Wunderlich, 2004: Cocalodini, Cocalodinae
Maddison, 2009: Cocalodinae

Remarks.—Cocalodines are non-salticine salticids with large PMEs (except in *Cucudeta* and *Depreissia*), restricted (except for *Depreissia*) to Australasia east of Wallace's Line (Wanless 1982; Maddison 2009). They are common components of the fauna of New Guinea, with varied body forms (Maddison 2009). Habitats vary, from foliage (*Cocalodes*, some *Tabuina*) to tree trunks (*Allococalodes*, *Yamangalea*, some *Tabuina*) and leaf litter (*Cucudeta*).

Monophyly: With the possible exception of the large size of the median apophysis (Maddison et al. in press), there are no known morphologieal synapomorphies of the group. However they are the only salticids east of Wallace's Line with a median apophysis on the palp. The molecular data (Maddison et al. 2014) clearly place the five Australasian genera together. The sixth genus, *Depreissia*, is placed only tentatively with the cocalodines. Known from central Africa and Borneo (Wesołowska 1997; Deeleman-Reinhold & Floren 2003; Szűts & Wesołowska 2003), *Depreissia* resembles an ant or wasp (Christa Deeleman-Reinhold, pers. comm.). Its placement outside the Salticinae is strongly supported by its median apophysis (Maddison et al. in press), absence of a cymbial apical groove cradling the embolus (Maddison et al. in press), and by molecular data (Maddison et al. in press). Molecular data suggest it is the sister group to the remaining cocalodines (Maddison et al. in press).

Tribe Lapsiini Maddison, **trib. nov.**
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:173197EF-71CA-4615-8786-4D33210B3BAC
(5 genera; Figs. 15–17)

Type genus.—*Lapsias* Simon, 1900

Remarks.—The Neotropical lapsiines are the only non-salticines other than lyssomanines in the New World. Following Simon's early description of four *Lapsias* species from Venezuela, no other species were correctly added to this group for more than a century. Recently, several species and four new genera were added (Maddison 2006, 2012; Makhan 2007; Ruiz & Maddison 2012; Ruiz 2013a). Some live on leaf litter (*Soesiladeepakius*, some *Lapsias*), others on foliage (*Galianora sachia* Maddison, 2006), others on mossy tree trunks (*Thrandina*, *Galianora bryicola* Maddison, 2006, other *Lapsias*). The only lapsiine with substantially large PMEs is *Thrandina*.

Monophyly and Diagnosis: There is no known morphological synapomorphy for this group. The molecular data strongly support its monophyly, although the unusual *Thrandina* branches deep (Maddison et al. 2014). Diagnostic characters can be found in the molecular data: in the alignments submitted by Maddison et al. (2014) to the Dryad data repository (http://dx.doi.org/10.5061/dryad.v53h1), site 110 in CO1 has G in *Thrandina parocula* Maddison, 2006 and the two species of *Galianora* (the only three lapsiines sampled for that gene) *versus* C in all other salticids sampled. Similarly, in 18S rRNA, sites 522 (A *vs.* G) and 543 (T *vs.* C) supply apparent synapomorphies for lapsiines.

Subfamily Eupoinae Maddison, **subfam. nov.**
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:BE3B9C99-A02F-40C4-8FF4-A20117EE2771
(3 genera; Figs. 21, 22)

Type genus.—*Eupoa* Żabka, 1985

Remarks.—Known from subtropical Southeast Asia (southern China, Vietnam, Thailand), these are the only known minute litter-dwelling non-salticines, resembling *Neon* or *Neonella*. Other litter-dwelling non-salticines (e.g., *Cucudeta*, *Soesiladeepakius*, some *Lapsias*) are larger-bodied. There are three genera described (Żabka 1985; Zhou & Li 2013a, b; Logunov & Marusik 2014). Their phylogenetic placement is uncertain, but both the molecular data and morphological features indicate they are non-salticines (Maddison et al. 2007, 2014). Zhou & Li (2013a, figs. 90, 91) illustrate the insertion of the highly complex palps into the epigynum.

Monophyly and Diagnosis: Eupoines can be recognized by the complex palps (Żabka 1985; Zhou & Li 2013a; Logunov & Marusik 2014), small size, the dorsal abdominal scutum in

the male, anterior eye row wider than posterior (Logunov & Marusik 2014), and the paired pale spots on the abdomen. The last two features could be synapomorphies, though they are weak. The complex palps will likely supply some morphological synapomorphies, but none has been clearly artieulated. Molecular data (Maddison et al. 2007, 2014) indicate that eupoines are distinctive from all of the other subfamilies, but these data do not give evidence for the monophyly of the group, as they are available for only one species (*Eupoa nezha* Maddison & Zhang, 2007). Logunov & Marusik (2014) suggest that the three genera are so close that they might best be considered a single genus. On the other hand, the apparent diversity in palp form is great.

Subfamily Hisponinae Simon, 1901
(9 genera; Figs. 23–27)

Simon, 1901: Hisponeae, Tomocyrbeae
Petrunkevitch, 1942: Gorgopsininae
Roewer, 1954: Hisponeae, Tomocyrbeae

Remarks.—The only extant subfamily of salticids recognizable in Baltic Amber, this group is diverse in Madagascar but nowhere else. Outside of Madagascar, the Seychelles and Afriea, they are known from only a few specimens from Asia (Wanless 1981a; Maddison & Piascik 2014). The constriction behind the small eyes is distinctive. This group has received attention in recent years (Wanless 1981a; Prószyński & Żabka 1983; Wesołowska 1993; Wesołowska & Haddad 2009, 2013, 2014; Szűts & Scharff 2009; Maddison & Piascik 2014), but many species remain to be described.

Monophyly: The transverse furrow or constriction in the carapace just behind the small eyes (Fig. 23) can be considered a synapomorphy of hisponines, as can the dual copulatory ducts in females (Maddison & Piascik 2014, figs. 21–23). Molecular data support the monophyly of the group (Maddison et al. 2014).

Relationships: Molecular and morphological evidence places the Hisponinae as the sister group to the Salticinae (Bodner & Maddison 2012; Maddison et al. 2014; Ramírez 2014). Morphological synapomorphies potentially uniting the two subfamilies are:

(1) Reduction of PMEs (Wanless 1984; homoplasious: also reduced in *Cyrba*, *Cucudeta*, *Lyssomanes*, *Onomastus*, *Pandisus*).
(2) Medial displacement of gnathocoxal glands (see Maddison 1996). In hisponines, the medial displacement can be seen in images of *Hispo* sp. (Bemaraha) (http://www.morphbank.net/bischen/?id=497568) in the SpiderATOL collection in MorphBank (M. Ramírez, http://www.morphbank.net/myCollection/?id=799626).
(3) Asymmetrical tarsal claws (Simon 1901: 385; Maddison 1996; Ramírez 2014).
(4) Female palp tarsal claw reduced (Ramírez 2014). In hisponines it is reduced to a nubbin (Ramírez 2014), in salticines lost entirely.
(5) Loss of conductor of palp (Ramírez 2014).
(6) Presence of a cymbial apical groove that cradles the tip of the embolus (Maddison et al. in press).

The first three of these had been considered synapomorphies of salticines by Maddison (1988, 1996), but at the time hisponines were unstudied (and indeed, implicitly considered as salticines).

Subfamily Salticinae Blackwall, 1841

Blackwall, 1841: Salticidae
Maddison, 1996: Saltieine Division
Maddison & Hedin, 2003a: Salticoida

Remarks.—This large clade, known in the past as the "advanced salticids" (e.g., Wanless 1984a), the "Salticine Division" (Maddison 1996), or the Salticoida (Maddison & Hedin 2003a), includes about 93% of the known species of salticids. Its former name Salticoida is reapplied in this classification to a narrower group excluding the Amycoida, so as to permit this major long-recognized clade to receive the formal rank of subfamily. Thus, the Salticinae is divided into two major clades, the Amycoida and the Salticoida. Salticines are known throughout the world, including temperate and arctic regions.

Monophyly: The monophyly of the Salticinae has been well demonstrated by both morphological (Maddison 1988, 1996; Ramírez 2014) and molecular data (Bodner & Maddison 2012; Maddison et al. 2014). The following ean be considered synapomorphies for the Salticinae:

(1) Tarsal claw absent on female palp (Maddison 1988, 1996; Ramírez 2014).
(2) Median apophysis absent on male palp (see Maddison 2009). It is also absent in some spartaeines, hisponines and lyssomanines. Some authors have interpreted structures in salticines as median apophyses (Logunov & Hereward 2006; Szűts & Rollard 2007; Logunov & Azarkina 2008b), but none appears homologous to that of basal salticids. The median apophysis of basal salticids is distinctive: a sclerite arising from the ventral face of the tegulum, surrounded by the tegulum but separated from it by a membrane, and with a special relationship to the spermophore (usually, a loop of the narrowing spermophore approaches the median apophysis before bending back and entering the embolus).
(3) Medial mound of slit sense organs on the chelicerae (Maddison 1988, 1996; Ramírez 2014).
(4) Inter-cheliceral sclerite reduced (Maddison 1988, 1996; Ramírez 2014).
(5) More complex tracheal system (Galiano 1976b; Wanless 1980c, 1981a; Ramírez 2014).
(6) An abrupt gait. Salticine locomotion is different from that of all or most non-salticines, involving motions that seem more abrupt. This could relate to the difference in tracheation. The gait difference has not been well

characterized, and so any synapomorphy cannot be described clearly, but an experienced collector can quickly recognize most non-salticines by their soft-edged, almost serene motions. Such a gait has been noted for the Spartaeinae (Maddison 2006, 2009) and Hisponinae (https://www.youtube.com/watch?v=HXDkUkLnK5g).

(7) Cymbium constricted at tibial joint, usually with distinct prolateral notch (Edwards in press).

The following may be synapomorphies of salticines, but have not been studied in enough members (e.g., in amycoids) to know where on the phylogeny they evolved:

(8) Loss of tarsal scopula of tenant setae (Ramírez 2014, character 161).

(9) Loss of trichobothrial distal plate transverse ridge (Ramírez 2014, character 182).

(10) Reduction of male PMS minor ampulates to one (Ramírez 2014, character 274).

(11) Loss of cymbium dorsal chemosensory patch (Ramírez 2014, character 324).

The following are derived features present in Salticinae but absent in most or all non-salticines. They have not been examined in hisponines, and therefore could be synapomorphies either for Salticinae, or for the clade uniting Salticinae and Hisponinae.

(12) Retinal strip of AME boomerang-shaped (as opposed to straight) (Blest et al. 1990).

(13) AME rhabdomeres rotated to eliminate suture lines (Blest et al. 1990).

A shorter and more anteriorly placed dorsal apodeme (fovea) of the carapace may also provide a synapomorphy (Wanless 1984). As well, salticines have, in general, greater heterogeneity of setae on legs than non-salticines. Salticine legs show a seemingly chaotic variety of setal lengths in addition to macrosetae, scales, and trichobothria. In contrast, the leg setae of many or all non-salticines appear as a uniform pelt. As with gait, differences in setae are not thoroughly studied.

Clade Amycoida Maddison & Hedin, 2003
(63 genera; Figs. 28–55)

Maddison & Hedin, 2003a: Amycoida

Remarks.—This diverse clade dominates the Amazon basin and stands as a major group in salticids — sister group to the enormous Salticoida — and yet is absent from the Old World except for *Sitticus*. Their body forms span the range of salticid diversity: long legged foliage-dwellers (the Amycini), ant-like forms (*Synemosyna*, *Sarinda*), beetle-like forms (*Cylistella*), flat bark dwellers (*Breda*), and unremarkable ground-dwellers (*Sitticus*). Most of what we know about the group is due to the efforts of Galiano (1957, 1958, 1963b, 1964a, b, c, 1965, 1966a, b, 1968b, 1971a, b, 1975, 1976a, 1977, 1985, 1987, 1988, 1989, 1991a, b), and more recently, Ruiz and colleagues (Ruiz & Brescovit 2005a, 2006a, b, 2013; Costa & Ruiz 2014; Patello & Ruiz 2014; Ruiz & Maddison in press). There are about 430 described species, but this is almost certainly only a small fraction of the total extant. For instance, there are currently 11 species of *Amycus* recognized from all of the Neotropics, but in about two months of collecting within a 10 km radius at Cuyabeno, Ecuador, I found about 20 species.

In each of the 9 contained tribes except the Gophoini and the Bredini, the palpal bulb has a fixed embolus and is usually circular, though occasionally oval.

Definition: A formal definition was given by Ruiz & Maddison (in press): the Amycoida is the smallest clade containing *Cotinusa*, *Amycus*, *Sitticus*, *Breda*, *Sarinda* and *Synemosyna*.

Here I follow the classification of Ruiz & Maddison (in press), except for the re-ranking of their subfamilies as tribes. As they treat the amycoids fully, the account here is abbreviated. See Ruiz & Maddison (in press) for synapomorphies and molecular support for the individual tribes.

Monophyly: This group was first recognized on the basis of molecular data, which strongly support its monophyly (Maddison & Hedin 2003a; Bodner & Maddison 2012; Maddison et al. 2014; Ruiz & Maddison in press). To date, there is no known morphological synapomorphy, though an unusual loop of the sperm reservoir of the palp is present near the subtegulum (Galiano 1968b, fig. 2; Prószyński 1980, fig. 5; Ruiz & Brescovit 2013, fig. 17 [left side]). It is rare to see such a loop in salticids with circular and fixed-embolus palps. Euophryines and others have a similar loop, but usually further from the subtegulum than in amycoids (Ruiz & Maddison in press).

Molecular data (Maddison, unpublished) show that *Asaracus*, once thought to be an amycoid (Ruiz & Brescovit 2008b), is a freyine near *Chira*. *Orvilleus* and *Toloella* are amycoids by their genitalia, but they are poorly studied and cannot yet be assigned to a tribe. *Albionella* and *Udahmella*, listed as Salticinae *incertae sedis*, could be amycoids.

Tribe Gophoini Simon, 1901
(8 genera; Figs. 28–30)

Simon, 1901: Thiodineae [based on a misinterpretation of *Thiodina*], Gophoeae
Petrunkevitch, 1928: Thiodininae
Roewer, 1954: Thiodininae, Thiodineae
Ruiz & Maddison, 2015: Gophoinae

Remarks.—This group, long known as the thiodinines, cannot retain that name with the discovery that the name *Thiodina* had long been misapplied (Bustamante et al. 2015; Ruiz & Maddison in press). Thus, Thiodineae and Thiodininae are not synonyms of Gophoini, but are listed in the synonymy above because the literature's past concept of Thiodininae refers to this clade. The type genus is *Gophoa* Simon, 1901, currently considered a junior synonym of *Cotinusa* Simon, 1900 (see Ruiz & Maddison in press). The best-known genus is *Colonus* (formerly known as *Thiodina*). Gophoines are elongate, often with a carapace-leg stridulatory apparatus (Maddison 1987) and paired bulbous setae on the first legs (Hill 2012). While their motions are often deliberate and slow, they are excellent jumpers, seeming to tense strongly before popping in long jumps.

Tribe Sitticini Simon, 1901
(10 genera; Figs. 32–34)

Simon, 1901: Sitticeae

Petrunkevitch, 1928: Sitticinae
Roewer, 1954: Sitticinae, Sitticeae
Prószyński, 1976: Sitticinae
Ruiz & Maddison, 2015: Sitticinae

Remarks.—This is the only amycoid group to have reached the Old World. The bulk of its described species are in Eurasia, studied extensively by Prószyński (1968, 1971b, 1973, 1980). However, the deeper diversity of the group is South American (Galiano 1987, 1989, 1991a, b; Ruiz & Brescovit 2005a, 2006a, b). Sitticines are distinctive in having lost the retromarginal chelicer al tooth (as in leptorchestines and some euophryines and aelurillines) and in having third legs much shorter than the fourth. They are ground dwellers, with few exceptions (e.g., *Sitticus palustris* (Peckham & Peckham, 1883) lives on marsh vegetation).

Tribe Bredini Ruiz & Maddison, 2015
(2 genera; Fig. 31)

Ruiz & Maddison, 2015: Bredinae

Remarks.—These flat salticids dwell in suspended litter and on tree trunks. Two genera are described (Ruiz & Brescovit 2013). They were once thought to be marpissines (e.g., Edwards 2006) but molecular data have shown them to be amycoids. In retrospect, the sperm duct loop in the tegulum is typical for amycoids (Ruiz & Brescovit 2013, fig. 15).

Tribe Scopocirini Simon, 1901
(2 genera; Figs. 39, 40)

Simon, 1901: Scopocireae
Roewer, 1954: Scopocireae
Ruiz & Maddison, 2015: Scopocirinae

Remarks.—The chelicerae and palps of males are unusual in *Scopocira* (Costa & Ruiz 2014). *Gypogyna* is only tentatively placed with *Scopocira* (Ruiz & Maddison in press).

Tribe Thiodinini Simon, 1901
(9 genera; Figs. 36–38)

Simon, 1901: Thiodineae
Simon, 1903: Hyetusseae
Mello-Leitão, 1917: Arachnomureae
Roewer, 1954: Hyetusseae
Ruiz & Maddison, 2015: Thiodininae

Remarks.—The name "Thiodinini" now applies to what would have formerly been called the Hyetusseae (Ruiz & Maddison in press), because of the reinterpretation of *Thiodina* (Bustamante et al. 2015). The thiodinines include both elongate (e.g., *Cyllodania*, *Arachnomura*) and high-bodied (e.g., *Titanattus*) forms (Ruiz & Maddison in press).

Tribe Sarindini Simon, 1901
(7 genera; Figs. 47, 48)

Simon, 1901: Sarindeae, Zuningeae [sic]
Roewer, 1954: Sarindeae, Zunigeae
Ruiz & Maddison, 2015: Sarindinae

Remarks.—Of the two major groups of ant-like amycoids, the sarindines are the more robust, appearing more like *Formica* or *Camponotus* ants than does *Synemosyna*.

Tribe Simonellini Peckham, Peckham & Wheeler, 1889
(4 genera; Figs. 41–46)

Peckham, Peckham & Wheeler, 1889: Simonellii
Banks, 1892: Synemosinae
F.O. Pickard-Cambridge, 1900: Synemosyneae
Simon, 1901: Synemosyneae
Roewer, 1954: Synemosyneae
Prószyński, 1976: Synemosyninae
Ruiz & Maddison, 2015: Simonellinae

Remarks.—This group is a strange mix of small beetle-like salticids (*Cylistella*, Figs. 44, 45) and ant-like salticids (Figs. 41–43, 46), including *Synemosyna*, often an excellent mimic of the elongate ant *Pseudomyrmex*. See Ruiz & Maddison (in press) for the use of the name "Simonellini". The type genus is *Simonella* Peckham & Peckham, 1885, a junior synonym of *Synemosyna* Hentz, 1846.

Tribe Huriini Simon, 1901
(6 genera; Fig. 35)

Simon, 1901: Hurieae
Ruiz & Maddison, 2015: Huriinae

Remarks.—Most huriines have a typical, unremarkable salticid body form (Fig. 35). Huriines have been studied by Galiano (1985, 1988).

Tribe Amycini F.O. Pickard-Cambridge, 1900
(13 genera; Figs. 49–55)

F.O. Pickard-Cambridge, 1900: Amyceae
Simon, 1901: Amycieae
Petrunkevitch, 1928: Magoninae
Roewer, 1954: Magoninae, Amycieae
Maddison & Hedin, 2003a: Amycinae
Ruiz & Maddison, 2015: Amycinae

Remarks.—This large and speciose group of mostly foliage-dwellers includes many with translucent legs, and males with a high clypeus. Many are excellent jumpers: I measured a 5.2 mm juvenile *Hypaeus* aff. *porcatus* (Taczanowski, 1871) from Yasuní, Ecuador jump 25 cm on a horizontal surface (more than 45 times its body length). The third leg is longer than the fourth (Ruiz & Maddison in press), as in many Simonida.

Clade Salticoida Maddison & Hedin, 2003, **new delimitation**
(427 genera; Figs. 56–136)

Remarks.—This clade, sister group to the primarily-Neotropical Amycoida, includes the vast bulk of described species in the Salticinae, although our counts are likely skewed against the Amycoida by the relatively little attention paid to the South American fauna. The relationships among the subgroups of Salticoida are ambiguous, but some analyses (Bodner & Maddison 2012) suggest that baviines, marpissoids

and astioids may form a clade, which would then be sister to the Saltafresia.

Definition: This clade has been recognized (e.g., node 3, Maddison et al. 2014), but not previously given a name. The name "Salticoida" is used for it here, reassigning the name from its former meaning (the current Salticinae), as explained under Salticinae. The Salticoida is now defined formally as the smallest clade containing baviines, marpissoids, astioids and the Saltafresia.

Monophyly: There are no known morphological synapomorphies of this group, and yet it is reconstructed with confidence by combined molecular datasets as well as by individual genes (28S rRNA, 18S rRNA, *wingless*, myosin HC; Maddison et al. 2014).

Tribe Agoriini Simon, 1901
(2 genera; Figs. 56, 57)

Simon, 1901: Agorieae
Petrunkevitch, 1928: Agoriinae
Roewer, 1954: Agoriinae

Remarks.—This group includes only *Agorius* and *Synagelides*, unusual ant-like saltieids from Asia and Australasia (Szűts 2003a; Logunov & Hereward 2006; Prószyński 2009a). *Agorius* holds the first legs curled and raised in life, like antennae (Fig. 56). The relationships of the group are unclear by both morphological and molecular data, but evidence suggests they are within the sister group to amycoids, i.e., within the Salticoida (Maddison et al. 2014). Their current placement outside of the major clades Saltafresia, Marpissoida and Astioida reflects ignorance and not evidence for exclusion. We simply do not know their relationships, and they may fall within one of those groups. The multiple-genes salticine analysis of Maddison et al. (2014: fig. 18) places them as sister to the chrysillines, but not firmly so, as the group is placed elsewhere by other analyses and individual genes. The palps of some species are unusual, but the simpler ones (Prószyński 2009a, figs. 27, 28) resemble those of chrysillines or hasariines.

Monophyly: Synagelides and *Agorius* have a male palp with unusually-proportioned segments, the femur being smaller than the robust patella (e.g., Logunov & Hereward 2006, fig. 4). In addition, the first leg has a tibia that is usually bent dorsally and with macrosetae closely packed in the distal half (Prószyński 2009a, figs. 16–22). In addition to these apparent synapomorphies, molecular data place *Synagelides* and *Agorius* together (Maddison et al. 2014).

Tribe Baviini Simon, 1901
(3 genera; Figs. 58, 59)

Simon, 1901: Bavieae
Roewer, 1954: Bavieae

Remarks.—The baviines, elongate and resembling marpissines, are common on large-leaved plants and suspended litter in Southeast Asian forests. They are speciose, despite the paucity of species currently described. The palp is of typical oval form with a fixed embolus and tegular ledge (i.e., with a cleft running retrolaterally across the bulb from the base of embolus).

Monophyly: Although the elongate and flattened body form (Figs. 58, 59) is consistent, it may not provide a synapomorphy for the group, as the same body form may be plesiomorphic in the possibly related marpissoids. The palps are fairly consistent, with a fixed embolus (e.g., Żabka 1988, figs. 29, 37, 52), generally like viciriines or marpissines, but without any known distinctive features. Molecular data, however, show that *Stagetilus* and *Bavia* fall together (Maddison et al. 2014). *Piranthus* is placed tentatively here on the basis of the close similarity in body form and markings with many *Bavia*.

Clade Astioida Maddison, Bodner & Needham, 2008
(55 genera; Figs. 78–89)

Maddison, Bodner & Needham, 2008: Astioida

Remarks.—The astioids form one of the two major radiations of Australasia (the other, euophryines). The group is almost restricted to Australasia, the Pacific Islands, and Southeast Asia, with only *Neon* and *Myrmarachne* having extended beyond to Europe, Africa and the Americas. Alongside the Marpissoida and Saltafresia, this is one of the three major subgroups of the Salticoida. The form of the body is varied, including the ant-like *Myrmarachne*, the robust beetle-like simaethines, the delicate astiines, and the majestic mopsines. This group has become known especially through the efforts of Żabka and colleagues (Żabka 1987a, 1990a, 1991a, b, 1992a, b, 1994, 1995, 2000, 2001, 2002, 2003, 2004, 2009, 2014; Żabka & Gray 2002, 2004; Gardzińska & Żabka 2010; Żabka & Patoleta 2014; Patoleta & Żabka 2015).

The division of the group into five tribes is based on the combined results of Maddison et al. (2008, 2014) and Bodner & Maddison (2012), which show a major subclade (here called the Viciriini) and four smaller clades outside that.

Definition: The group was proposed by Maddison et al. (2008). It is here defined formally as the smallest clade including *Neon*, *Myrmarachne*, *Mopsus*, *Astia*, *Viciria*, *Trite* and *Simaetha*.

Monophyly: There are no known morphological synapomorphies, but the Astioida is well supported by molecular data (Maddison et al. 2008, 2014; Bodner & Maddison 2012). The embolus is generally fixed to the tegulum, but in some there appears to be a movable embolus (*Neon*, *Mopsus*), which however is not spiralled in the same manner as euophryines or marpissoids.

Because of the diversity of genitalia in this group, it is difficult to assess which unsequenced salticid genera are in fact astioids. However, the biogeographical pattern is strong, and we can guess that any salticid with a fixed embolus occurring in Australasia that is not obviously a member of another group (e.g., not a plexippine or chrysilline) is likely to be an astioid. Thus, among the genera listed as Salticinae *incertae sedis*, I suspect that *Aruana*, *Grayenulla*, *Hinewaia*, *Maddisonia*, *Proszynellus*, *Pseudonaevia*, and *Pseudosynagelides* are all astioids. *Muziris* could also be an astioid.

Tribe Myrmarachnini Simon, 1901
(7 genera; Figs. 78, 79)

F.O. Pickard-Cambridge, 1900: Toxeae, Toxeinae
Simon, 1901: Myrmarachneae, Ligonipedeae
Petrunkevitch, 1928: Myrmarachninae
Roewer, 1954: Myrmarachninae, Myrmarachneae, Ligonipeae

Remarks.—The mymarachnines form the most speciose clade of ant-like jumping spiders, most species of which are in the enormous genus *Myrmarachne* (Galiano 1969; Wanless 1978a; Edwards & Benjamin 2009; Edwards 2013; Benjamin 2015). There is great variability in appearance: depending on the colour, and the width and contours of the body, different species resemble different groups of ants. *Myrmarachne* has been the focus of studies of mimicry (Nelson et al. 2005; Edmunds 2006; Ceccarelli & Crozier 2007; Ceccarelli 2008; Nelson & Jackson 2009b; Huang et al. 2011), social behavior (Jackson et al. 2008a; Nelson & Jackson 2008), predatory behavior (Jackson 1986c; Jackson & Willey 1994), and sexual selection (Pollard 1994). Apart from a few Neotropical species of *Myrmarachne*, the group is entirely Old World. Edwards & Benjamin (2009) present a review of the group with a morphological phylogeny.

The name Toxeinae is not used as it was replaced, before 1961, by Myrmarachneae/Myrmarachninae because of synonymy of the type genus (ICZN 1999, article 40.2).

Monophyly: The morphological features that confer their striking resemblance to ants — e.g., narrow body with constrictions in the thorax — are synapomorphies, although they have evolved elsewhere in the family several times. Most distinctive, then, are the genitalia. The bulb is round, with the fixed embolus looping one or more times around it. Instead of faithfully following the periphery of the bulb, some loops of the embolus typically fall beneath and across the tegulum (e.g., Edwards & Benjamin 2009, figs. 4A, C, 7). The epigynum has a stereotyped arrangement, with the loops of the copulatory ducts eventually reaching the midline near the posterior margin then proceeding together side by side to the anteriorly-placed fertilization ducts (Prószyński 1992b, figs. 87, 92; Edwards & Benjamin 2009, fig. 7).

Tribe Neonini Maddison, **trib. nov.**
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:69DB2118-1C16-41E3-B914-150E0B96435A
(1 genus; Fig. 80)

Type genus.—*Neon* Simon, 1876

Remarks.—Although initially familiar from the Holarctic region, *Neon* is now recognized as extending to Southeast Asia (Logunov 1998) and as having "radiated widely" in Australia (Richardson et al. 2006; Richardson 2013). It is not surprising, therefore, that molecular data have placed it in the primarily Australasian Astioida (Maddison et al. 2008).

Monophyly and Diagnosis: Small salticids with a relatively cubic carapace, a freely movable embolus (Logunov 1998, fig. 21) that is often spiraled (e.g., Gertsch & Ivie 1955, figs. 19, 24; Prószyński 1976, fig. 438), and long macrosetae under the first leg's tibia. One possible synapomorphy is the shift of the embolus to arise on the prolateral side of the bulb. Although this shift is often seen in species with a fixed embolus, it is less common among species with a freely movable embolus.

An undescribed second lineage of neonines, larger-bodied, has been found in New Guinea (Maddison, unpublished data). The genus *Ananeon* (Richardson 2013) may be a neonine.

Tribe Astiini Simon, 1901
(11 genera; Figs. 82, 83)

Simon, 1901: Astieae
Roewer, 1954: Astieae

Remarks.—This tribe more or less matches Wanless's Astieae (1988), as supplemented by Żabka (1995, 2009) and Prószyński & Deeleman-Reinhold (2010). Typically long-legged and somewhat delicate-bodied, these spiders are Australasian and Southeast Asian. The astiine *Orthrus* was formerly placed with lyssomanines (Simon 1901), based on its eye placement and delicate translucent green body (Fig. 82).

Monophyly: The palp has a simple bulb, with embolus and tegulum fused and typically without elaboration. Wanless (1988) gives as two of their characteristics that they are pluridentate, and that they have the posterior lateral eyes "separated from lateral margins of the carapace by a distinct space when viewed from above" (e.g., Wanless 1988, fig. 9A). Although these characteristics in themselves might give little confidence in monophyly, molecular data support the group (Maddison et al. 2008).

Żabka (2009) suggests *Astilodes* may belong in the Astieae. Żabka (1995) places *Megaloastia* within the Astieae. *Parahelpis* is closely similar to *Helpis* (Gardzińska & Żabka 2010). Prószyński & Deeleman-Reinhold (2010) suggest *Katya* may belong to the Astieae, and indeed it has close similarities in its body and genitalia with *Orthrus*, particularly the overhanging lip of the epigynum and spermathecal configuration.

Tribe Mopsini Maddison, **trib. nov.**
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:99FA80D3-FF59-4C84-A1C7-347D280D0077
(3 genera; Fig. 81)

Type genus.—*Mopsus* Karsch, 1878

Remarks.—This group of Australasian salticids includes just a handful of species in three genera, and yet is familiar through the often-photographed *Mopsus*.

Monophyly and Diagnosis: Large and robust Australasian salticids, with the embolus arising hidden behind the distal end of the tegulum and directed obliquely retrolateral (Żabka 2000, fig. 2). Żabka (2000) recognized the relationship of *Mopsus*, *Sandalodes*, and *Mopsolodes*, noting the similarities in male palps. The embolus appears movable, with a distinct embolic hematodocha (Maddison, unpublished data). Molecular data confirm the relationship of *Mopsus* and *Sandalodes* (Maddison et al. 2008). Those molecular data had suggested *Clynotis* was also closely related, which would be puzzling as *Clynotis* has a rather different embolus, possibly immovable. However, reexamination has shown that the 28S rRNA sequence used for *Clynotis severus* (L. Koch, 1879) by Maddison et al. (2008) is almost certainly a contaminant, as it is identical to that of the specimen of *Sandalodes scopifer* (Karsch, 1878). When reanalyzed with this sequence excluded, *Clynotis* groups more reasonably with the viciriines *Ocrisiona jovialis* (L. Koch, 1879) and *Holoplatys*.

Tribe Viciriini Simon, 1901
(33 genera; Figs. 84–89)

Simon, 1901: Vicirieae, Rogmocrypteae
Simon, 1903: Triteae, Simaetheae
Roewer, 1954: Triteae, Rogmocrypteae, Simaetheae, Vicirieae

Remarks.—Members of this tribe show many body forms, including the elongate *Viciria*, the wide-bodied *Simaetha*, the flat *Holoplatys*, and the more mundane *Trite* and *Opisthoncus*.

One distinctive group, the simaethines, is separated as a subtribe. The remaining viciriines are diverse enough to deserve subdivision, but their phylogenetic relationships are too poorly known to assign them to subtribes even tentatively. The consequence of this is that *Viciria* is (necessarily) within the subtribe Viciriina, but all other non-simaethine vieiriines remain as Viciriini *incertae sedis*. Of the four Simon group names that could apply to this tribe, Viciriini is chosen as it has priority over Triteae and Simaetheae (appearing in 1901 with diagnostic characters in the key of p. 517) and *Viciria* is better known than *Rogmocrypta*.

Monophyly: There are no known morphological synapomorphies of this group. The most comprehensive molecular data (Maddison et al. 2014) put *Trite*, *Nungia* and the simaethines together, while other studies (Maddison et al. 2008; Bodner & Maddison 2012) add to these *Viciria*, *Corambis*, *Holoplatys*, *Opisthoncus*, *Penionomus*, *Rhondes*, and some of their relatives. See note under Mopsini regarding molecular support for *Clynotis* being a viciriine.

Paraplatoides, *Zebraplatys*, *Holoplatys* and *Ocrisiona* are considered by Żabka (1992a) to form a monophyletic group. Żabka and Gray (2004) suggest *Huntiglennia* is related to *Zebraplatys*. Prószyński (2015) suggests that *Avarua* may be *Trite*, and indeed it resembles the vieiriine *Corambis*. Żabka (1987a) concludes that *Tara* is closely related to *Clynotis*. By both body and genitalia, *Clynotis albobarbatus* L. Koch, 1879 and *Diplocanthopoda hatamensis* (Thorell, 1881) appear to be close to, or belong within, *Nungia*, of which there are several undescribed species in New Guinea (Maddison, unpublished data). The molecular data from cf. *Lystrocteisa* and cf. *Rogmocrypta* (Maddison et al. 2008) suggest that *Lystrocteisa* and *Rogmocrypta* are viciriines, at least if similarities of the sequenced specimens to those genera represent relationship. Two additional genera are included tentatively within the Viciriini, *Abracadabrella* and *Paraphilaeus*. Their placement is based on the fact that they resemble viciriines like *Opisthoncus* in having paired abdominal markings resembling those of dendryphantines, along with palps generally resembling some viciriines. It is likely the case that several other Australasian genera like *Grayenulla* (Żabka 1992b) and *Hinewaia* (Żabka & Pollard 2002a) are also viciriines, but the data are unclear, and they are left as Salticinae *incertae sedis*.

Subtribe Simaethina Simon, 1903
(13 genera; Figs. 87, 88)

Simon, 1903: Simaetheae
Roewer, 1954: Simaetheae

Remarks.—These wide-bodied, often beetle-like salticids are distinctive components of Southeast Asian and Australasian faunas. They form a subgroup of the Viciriini.

Monophyly: The palp's bulb is round to oval, with a short embolus (e.g., Prószyński 1984a, p. 77, 1987, p. 107; Żabka 1994, fig. 1B). Among salticids with a fixed embolus, only the simaethines have such wide bodies with robust carapaces, with the exception of the tiny *Cylistella* in the amycoids. There are other salticids with such a wide body (e.g., *Beata*, *Coccorchestes*, *Omoedus*, *Pachyballus*, *Rhene*, *Rhetenor*), but these are marpissoids or euophryines, with a freely movable embolus. The molecular data confirm that the wide-bodied astioids form a clade (Bodner & Maddison 2012; Maddison et al. 2014, unpublished data).

Urogelides is included as it appears close to *Uroballus*, sharing elongate spinnerets (Żabka 2009). *Iona* is placed by Prószyński (2015) with the simaethines. *Simaethula* is considered by Żabka (1994) to be a relative of *Simaetha*. The type species of *Stertinius* is not well known, but other species placed in the genus (Prószyński & Deeleman-Reinhold 2013) share the unusual cymbial extension of some *Itura* species (Peng et al. 1993). Having robust bodies and genitalia typical of simaethines are *Mantius* (Workman & Workman 1894; Prószyński 1984a), *Phyaces* (Wanless 1986), *Porius* (Prószyński 1984a), and *Poecilorchestes* (Prószyński 1971a). *Flacillula*, *Microhasarius*, *Pilia*, *Simaethulina*, and *Stergusa*, listed as Salticinae *incertae sedis*, could also be simaethines. *Stergusa*, at least for the species described by Prószyński & Deeleman-Reinhold (2010), has the palp typical of a simaethine, but at the same time these are very similar in body and palp to the euophryine *Sobasina*. The placements of *Microhasarius* and *Pilia* are especially important to resolve, as an available family-group name (Simon 1903) is based on each.

Clade Marpissoida Maddison & Hedin, 2003
(90 genera; Figs. 60–77)

Maddison & Hedin, 2003a: Marpissoida

Remarks.—Although the largest tribe of marpissoids (Dendryphantini) is primarily a New World group, the other two tribes are restricted to the Old World (ballines and tisanibines).

Definition: After its original conception, Marpissoida was expanded to include the ballines (Bodner & Maddison 2012) and then the tisanibines (Zhang & Maddison 2014). However, given that the placement of tisanibines with the marpissoids is not made with full confidence (Zhang & Maddison 2014), the definition of the Marpissoida will be conditional: The Marpissoida is the smallest clade containing the Dendryphantina, Marpissina, Ballini and the Tisanibini, except if *Tisaniba* is not a close relative of the other three, in which case the Marpissoida would be the smallest clade containing the Dendryphantina, Marpissina, and Ballini.

Monophyly: The embolus is ancestrally spiral and movable, with a well-developed embolic hematodocha. The spiral typically appears edge-on in ventral view (Maddison 1996, fig. 64e; Edwards 1999, fig. 14), as its axis is parallel to the axis of the palp, unlike that of euophryines whose axis is usually perpendicular to that of the palp (Zhang & Maddison 2015). A simple open spiral is seen in ballines, tisanibines, synagelines and itatines, while a compacted spiral is seen in dendryphantines (Maddison 1996). Within the Marpissina, however, the embolus has become secondarily fixed. While the spiral embolus and the full development of the embolic hematodocha could be synapomorphies of the Marpissoida, they are also present in hisponines (Szűts & Scharff 2009) and euophryines (Zhang & Maddison 2015). The marpissoids are well supported by

molecular data (Bodner & Maddison 2012; Maddison et al. 2014) with some ambiguity about the inclusion of tisanibines (Zhang & Maddison 2014; Maddison et al. 2014).

Tribe Ballini Banks, 1892
(15 genera; Figs. 60–63)

Banks, 1892: Ballinae
Simon, 1901: Balleae, Copocrosseae
Roewer, 1954: Balleae, Copocrosseae
Benjamin, 2004: Ballinae

Remarks.—Members of this Old World group have unusual and varied body forms, with some resembling beetles (*Ballus*, *Pachyballus*), others ants (*Afromarengo*, *Leikung*, *Marengo*). Two contrasting extremes are the wide-bodied *Pachyballus* and the narrow and tailed *Mantisatta* (Cutler & Wanless 1973). Benjamin (2004) reviews the group and its phylogeny. Andriamalala (2007) found that convergent evolution of remarkable cheliceral horns in *Padilla* was uncorrelated with environment, suggesting the action of sexual selection.

Monophyly: Benjamin (2004) lists 6 putative morphological synapomorphies for the ballines: (1) an embolic coil of more than 360°, lying flat on the tegulum; (2) a subtegulum that extends over the tibia; (3) a narrow septum on the epigynum, (4) long copulatory ducts and spermatheca with internal spicules; (5) an enlarged femur 1 with dark lateral bands; and (6) small to medium body size with enlarged tibia 1. However, the primary argument for these comes from an analysis that included just one outgroup taxon, and therefore cannot speak to the monophyly of the group. Trait (1) is seen in synagelines and tisanibines, while (3), (4), (5) and (6) are seen in other salticids. Nonetheless, among Old World salticids, ballines are recognizable for the embolus, the pale longitudinal trough on the tegulum (Benjamin 2004, fig. 20A), robust first legs, and resemblance to beetles, pseudoscorpions, or ants. The molecular data suggest they are indeed monophyletic (Bodner & Maddison 2012), although these studies do not include the atypical *Cynapes*.

Among the genera listed as Salticinae *incertae sedis*, *Ligdus* could be a balline, and *Houalattus* could be either a balline (*Pachyballus*), or a dendryphantine (*Rheue*).

Tribe Tisanibini Maddison, **trib. nov.**
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:9A96C04C-E0B5-42CB-8D8E-5F7AFAC79133
(2 genera; Figs. 64, 65)

Type genus.—*Tisauiba* Zhang & Maddison, 2014

Remarks.—Tisanibines are small leaf-litter dwellers in tropical forests of Southeast Asia. Although common in some areas (Zhang & Maddison 2014), they were entirely undescribed until recently (Logunov & Azarkina 2008b; Zhang & Maddison 2014).

Monophyly and Diagnosis: As in other marpissoids such as ballines and synagelines, the embolus is a spiral with axis parallel to that of the palp (Zhang & Maddison 2014). The body form is unusual among marpissoids, however, as the males are small, black, shiny, and with a dorsal abdominal scutum (Fig. 65). Molecular data (Zhang & Maddison 2014) show that *Tisauiba* is outside the Ballini and the Dendryphantini. A molecular synapomorphy of tisanibines is suggested by the broad sample alignments submitted by Zhang & Maddison (2014) to the Dryad data repository (http://dx.doi.org/10.5061/dryad.984fn), wherein site 138 of the 28S rRNA alignment has A in all four tisanibines sampled and different bases in other salticids.

Of the two genera placed here, *Tisaniba* and *Saaristattus*, the former is chosen as the type genus, rather than the older name *Saaristattus*, because the molecular data justifying the group's placement come from the type species of *Tisaniba*, and *Saaristattus* is only tentatively associated with *Tisaniba*.

Tribe Dendryphantini Menge, 1879
(73 genera; Figs. 67–77)

Menge, 1879: Dendryphantidae
See also listings under subtribes

Remarks.—The Dendryphantini, including the synagelines, itatines, marpissines and dendryphantines proper, matches the original content of the Marpissoida (Maddison & Hedin 2003a), before ballines and tisanibines were added to the latter by Bodner & Maddison (2012) and Zhang & Maddison (2014). The Dendryphantini are primarily in the New World.

Monophyly: There are no known morphological synapomorphies. The monophyly of the group is well supported by molecular data (Hedin & Maddison 2001; Maddison & Hedin 2003a; Maddison et al. 2014).

Semoriua by genitalia appears to be in the Dendryphantini (Gustavo Ruiz, pers. comm.), but within which subtribe is unclear.

Subtribe Synagelina F.O. Pickard-Cambridge, 1900
(6 genera; Figs. 67–70)

F.O. Pickard-Cambridge, 1900: Synageleae
Simon, 1901: Synageleae, Peckhamieae
Petrunkevitch, 1928: Synagelinae, Peckhamiinae
Roewer, 1954: Synagelinae, Synageleae, Peckhamiinae

Remarks.—In parallel to the ballines, this group's morphological spectrum extends from forms resembling ants (*Synageles*, *Peckhauia*) to beetles (*Attidops*) and pseudoscorpions (*Admestina*, *Cheliferoides*). The ant-like species are unusual in waving the second pair of legs like antennae (Fig. 68), rather than the first, which is typical for other ant-like salticids. Except for some species of *Synageles*, synagelines are entirely New World (Platnick 1984; Cutler 1988; Piel 1992; Edwards 1999).

Monophyly: There are no clear morphological synapomorphies of the group as a whole. The embolus typically is distinctly spiralled, in some cases winding several times, resembling many ballines (Edwards 1999). Molecular data support the group (Bodner & Maddison 2012; Maddison, unpublished data).

The second leg of *Descanso* has a darkened tip and is held aloft while walking (Gustavo Ruiz, unpublished data), which, combined with the body form and the spiral embolus (Galiano 1963a, 1986), confirm its placement in the Synagelina.

Subtribe Itatina Simon, 1901
(1 genus; Fig. 66)

Simon, 1901: Itateae
Petrunkevitch, 1928: Itatinae
Roewer, 1954: Itatinae, Itateae

Remarks.—A single Neotropical genus of elongate spiders, green or yellowish, resembling baviines. It is here considered a distinet tribe as it falls outside the other major groups (Maddison & Hedin 2003a; Maddison et al. 2008; Zhang & Maddison 2014), without a clear sister group relation to any of them.

Monophyly: Although there are no described morphological synapomorphies for *Itata*, its species are recognizable by their elongate shape and yellow-green colour (Fig. 66) among New World salticids. The embolus has a distinct spiral.

Subtribe Marpissina Simon, 1901
(9 genera; Figs. 71, 72)

Banks, 1892: Marptusi
F.O. Pickard-Cambridge, 1900: Marptuseae
Simon, 1901: Marpisseae
Simon, 1903: Maevieae
Petrunkevitch, 1928: Marpissinae, Maeviinae
Roewer, 1954: Marpissinae, Marpisseae, Maeviinae, Maevieae
Prószyński, 1976: Marpissinae

Remarks.—This mostly New World group includes many tree trunk or suspended litter dwellers, in contrast to the primarily foliage-dwelling dendryphantines. The North American *Maevia inclemens* (Walekenaer, 1837) is notable for having strikingly dimorphic males (Peckham & Peckham 1889; Painter 1913; Clark & Uetz 1992, 1993; Clark 1994; Clark & Morjan 2001; Clark & Biesiadecki 2002).

The old name Marptusi Banks was based on *Marptusa* Thorell, 1877, an unjustified replacement for *Marpissa* C.L. Koch, 1846 (Simon 1903), and thus a junior objective synonym thereof. On this basis, Simon (1901) rejeeted Marptusi and preferred Marpisseae. The preferenee for Marpisseae is therefore to be maintained (ICZN 1999, article 40.2).

Monophyly: The palp is narrow and in general resembles that of dendryphantines, but in many marpissines (e.g., *Fuentes* and *Balmaceda*, Edwards 2006), the embolie hematodocha is reduced and the embolus fixed to the tegulum and not spiral, presumably representing a secondary loss of the movable spiral embolus. However, this does not provide a synapomorphy for the group as a whole. Among New World salticids the group can be partially recognized by the general form of the palp and the slightly flattened or elongate body (Figs. 71, 72), but this simple characterization led us astray with *Breda*, assumed to be a marpissine by its resemblance to genera such as *Fuentes*, but in fact an amycoid (Ruiz & Maddison in press). Molecular data support the Marpissina (Maddison & Hedin 2003a).

The group was recognized approximately by Barnes (1958), but he included *Menemerus*, since shown to be a chrysilline (Maddison & Hedin 2003a). The concept of the group here is almost precisely that of Edwards (2006), with the exception that he included *Breda*. *Mendoza* is closely related to *Marpissa* (Logunov 1999b). Gustavo Ruiz (pers. comm.) indicates that *Empanda* is a marpissine.

Subtribe Dendryphantina Menge, 1879
(56 genera; Figs. 73–77)

Menge, 1879: Dendryphantidae
Banks, 1892: Phidippi
F.O. Pickard-Cambridge, 1900: Phidippeae
Simon, 1901: Dendryphanteae, Rheneae
Simon, 1903: Rudreae, Zygoballeae
Petrunkevitch, 1928: Dendryphantinae, Zygoballinae
Roewer, 1954: Dendryphantinae, Dendryphanteae, Donaldieae, Rheneae, Rudreae, Zygoballinae, Zygoballeae
Prószyński, 1976: Dendryphantinae

Remarks.—Although well known in Eurasia for *Dendryphantes, Rhene,* and *Macaroeris*, this group is primarily from the Americas (Maddison 1996). Dendryphantines dominate the species diversity of salticids in many areas of North America. The largest subclade consists of high-bodied and reasonably robust spiders such as *Phidippus* and *Dendryphantes*; outside of that is a series of less speciose lineages that include more elongate or flattened spiders such as *Hentzia* and *Phanias* (Hedin & Maddison 2001). *Phidippus* (Edwards 2004) includes some of the largest salticids in the world, sometimes exceeding 20 mm in length while also being broad and high-bodied. *Phidippus* has been the subject of many studies, of movement and foraging (Givens 1978; Hill 1979, 2010a, b; Freed 1984; Edwards & Jackson 1993; Hoefler & Jakob 2006; Baker 2007; Stankowich 2009), vision and neurophysiology (Land 1969a, b; Hill 1975; Sivertson 1985; Jackson 1986a; Blest et al. 1988; Hoefler et al. 2002; Baker et al. 2009; Bednarski et al. 2012; Spano et al. 2012; Menda et al. 2014), learning and experience (Edwards & Jackson 1994; Skow & Jakob 2006; Jakob et al. 2007; Kasumovic et al. 2009), and mating behavior (Jackson 1977a, b, c, 1978, 1980a, b, c, d, e, 1981a, b, 1982; Edwards 1982; Robertson & Stephens 2002; Hoefler 2007, 2008; Elias et al. 2008, 2010; Sivalinghem et al. 2010). At least three separate lineages are in the Old World, represented by *Rhene*, *Macaroeris*, and *Dendryphantes*.

Monophyly: Maddison's (1996) composition of the Dendryphantinae, confirmed for many genera by molecular data (Hedin & Maddison 2001; Maddison & Hedin 2003a), was supported by several proposed synapomorphies: a carina on the underside of the male chelicera (Maddison 1996, fig. 10), the coil of the spiral embolus folded back so as to be hidden behind the base of embolus (Maddison 1996, fig. 64), and S-shaped epigynal openings (Maddison 1996, fig. 4). Males of many species have dark bodies with longitudinal white bands on either side of the thorax and continuing onto the abdomen (Fig. 77). Sexual dimorphism often involves enlarged chelicerae and first legs in males.

The genera listed here under Dendryphantina follow Maddison (1996), with some genera added, including *Pseudofluda* and *Naubolus* (Edwards et al. 2005). Gustavo Ruiz (pers. comm.) indicates that the poorly studied *Anokopsis*, *Alcmena*, *Pseudopartona* and *Monaga* are all dendryphantines. *Mirandia*, by Badcock's (1932) illustration, appears to be a dendryphantine. Based on the body form, shape of the palp and the sperm

duct loop, both *Planiemen* (Wesołowska & Harten 1994) and *Xuriella* (Wesołowska & Russell-Smith 2000) are provisionally considered to be close to *Rheue*, although if so the embolus would be modified from the typical form. The palps of the two known male specimens of *Tuvaphantes* are highly unusual, without a recognizable spermophore or embolus (Logunov 1993). I suspect they are teratologies, as they closely resemble deformed palps in other otherwise-identifiable salticids I have seen (Maddison, unpublished data). For example, Levi's illustration of the palp of *Phidippus opifex* (McCook, 1883) (= *P. octopunctatus* (Peckham & Peckham, 1883)) in Gardner (1965, fig. 1) shows a similar, presumably deformed palp (compare to Edwards' 2004 fig. 11 of the same species). *Homalattus*, listed as Salticinae *incertae sedis*, could be either a dendryphantine (*Rhene*) or a balline (*Pachyballus*).

Clade Saltafresia Bodner & Maddison, 2012
(277 genera; Figs. 90–136)

Bodner & Maddison, 2012: Saltafresia

Remarks.—The Saltafresia is the third and largest of the three major clades of the Salticoida *sensu stricto*. Despite the size of the group (more than 3000 species), it is rather conservative in body form, having relatively few species of ant-like, beetle-like, highly elongate or other unusual body forms. Saltafresians are largely Afro-Eurasian, with the exception of many euophryines and the freyines.

Although the molecular data are to some extent ambiguous, there is evidence for a subclade consisting of the Plexippini, Aelurillini, Leptorchestini, Salticini and the Euophryini (Bodner & Maddison 2012; Maddison et al. 2014, node 4). I name it here as the **Simonida**, in honour of Eugène Simon. It is formally defined as the smallest clade including the type genera of those 5 groups. Frequently seen among the Simonida are relatively robust legs — e.g., *Cytaea*, *Aelurillus*, *Freya*, *Pellenes*, *Evarcha*, *Hyllus*, *Plexippus* and *Yllenus*. Insofar as they might remind us of humans, these spiders appear as strong-legged athletes. Longer third legs, possibly accompanied by a shift in jumping mechanics, evolved several times in this subclade (e.g., Figs. 112, 117, 123, 125, 136; Otto & Hill 2012b).

Definition: The Saltafresia was defined by Bodner & Maddison (2012) as the smallest clade containing the Plexippini, the Aelurillini, Euophryini, Chrysillini, Leptorchestini, Hasariini, Salticini and *Nannenus*.

Monophyly: There is no known morphological synapomorphy of the Saltafresia, but the group is reasonably well supported by molecular data (Bodner & Maddison 2012; Maddison et al. 2014).

Tribe Nannenini Maddison, **trib. nov.**
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:235D0370-6EBD-4A5B-B190-31914A98C1BD
(3 genera; Figs. 97–99)

Type genus.—*Nannenus* Simon, 1902

Remarks.—This small Southeast Asian group makes up a poorly known but common component of Southeast Asian faunas, especially on leaf litter (Prószyński & Deeleman-Reinhold 2012; Maddison & Piascik, unpublished data). Only two generic names can be unequivocally assigned to the group (*Nannenus* and *Idastrandia*), but the number of genera is likely to grow as the many undescribed species become known.

Monophyly and Diagnosis: The macrosetae under the first tibia tend to be long (Szombathy 1915, fig. 5d; Prószyński 1987, p. 69), as in some thiratoscirtines and *Neon*, but this may be merely an adaptation to litter-dwelling. The embolus is fixed to the tegulum (Prószyński 1983b, fig. 7; Prószyński & Deeleman-Reinhold 2012, figs. 98, 100), with the possible exception of *"Bathippus" pahang* Zhang, Song & Li, 2003. Neither the macrosetae nor fixed embolus provides a clear synapomorphy for the group. Nonetheless, molecular data unite them (Zhang & Maddison 2013; Maddison et al. 2014, unpublished data), and they are relatively easy to recognize by being small to medium-sized compact-bodied salticids, relatively setose, Southeast Asian, and with an embolus that is generally more delicate than that of the hasariines. In the concatenated alignment submitted by Bodner & Maddison (2012) to TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S13034) are two synapomorphies for nannenines, with site 737 (within 28S rRNA) showing T in nannenines *versus* C in others, and site 2171 (within ND1) showing C *vs.* T.

Langerra is placed here only tentatively because its type species has not been studied recently. Although the species of *Langerra* studied for molecular phylogeny by Maddison et al. (2014) is clearly close to *Langerra longicymbium* Song & Chai, 1991, sharing its distinctive cymbial projection (Song & Chai 1991, fig. 7E), the question remains whether *L. longicymbium* belongs with the type species *L. oculina* Żabka, 1985. Females of the species studied by Maddison et al. (2014) have an epigynum (Maddison, unpublished data) that resembles that of *L. oculina* in having openings placed laterally beneath a transverse fold, with ducts proceeding anteriorly (Żabka 1985). Thus, the studied species' molecular placement with nannenines can be provisionally considered to apply to *Langerra*. *"Bathippus" pahang* does not belong to the euophryine genus *Bathippus*; it is a nannenine (Zhang & Maddison 2013). Among the genera listed as Salticinae *incertae sedis*, *Epidelaxia*, *Lechia* and *Leuserattus* could be nannenines.

Tribe Hasariini Simon, 1903
(15 genera; Figs. 100–102)

Simon, 1903: Hasarieae
Petrunkevitch, 1928: Hasariinae
Roewer, 1954: Hasariinae, Hasarieae, Diplocanthopodeae

Remarks.—The cosmotropical *Hasarius adansoni* (Audouin, 1826) is the only widely known hasariine. In general they are ground dwellers, except for the trunk- or rock-dwelling *Gedea*. *Diplocanthopoda marina* Abraham, 1925 lives in the intertidal zone (Abraham 1925; Maddison, unpublished data). *Habrocestum* is reasonably speciose in Africa (Wesołowska & van Harten 1994, 2002, 2007; Wesołowska 2000, 2006b; Wesołowska & Russell-Smith 2000, 2011; Wesołowska & Haddad 2009; Haddad & Wesołowska 2013). Recent molecular work has assigned some small Southeast Asian genera to the group (Maddison et al. 2014). The single native New World species is the eastern North American *Chinattus parvulus* (Banks, 1895) (Edwards 2003a).

Monophyly: Hasariines are compact-bodied, often with distinctly white-edged palps that are held across the face. The palp's bulb is generally oval, with a reasonably robust embolus and a cleft across the face of the functional tegulum. A probable synapomorphy for the group is a small circular structure hidden in an overhanging lip at the back of the epigynum (see Logunov 1999a, figs. 17, 45), although a similar structure is seen in freyines (Edwards in press). Logunov (1999a) correctly surmises that *Chinattus* is related to *Habrocestum*. Although Logunov suggests that *Habrocestoides* is not near *Habrocestum* or *Chinattus*, the similarities to *Chinattus* in body form and genitalia, including the peculiar epigynal lip, suggest that *Habrocestoides* (for which molecular data are lacking) is a hasariine. The molecular data strongly link *Hasarius*, *Habrocestum*, *Chinattus*, and several other genera (Maddison et al. 2014).

Meata Żabka, 1985, known only from the female, is here synonymized with *Gedea* Simon, 1902 (**NEW SYNONYMY**), based on co-collecting and molecular data matching it with male *Gedea* (Maddison, unpublished data). *Curnbis* is likely close to, or a synonym of, *Echeclus* (Maddison et al. 2014). *Hasarina*, *Imperceptus*, and *Madhyattus* are placed here based on the epigynum's overhanging lip with a circular notch; *Hasarina* in addition has a typical hasariine palp. *Mikrus* and *Uxuma* are included because of the resemblance of the palp to hasariines, and *Mikrus* in addition has a body and markings that strongly resemble *Chinattus*. Among the genera listed as Salticinae *incertae sedis*, *Ghumattus*, *Heliophanoides*, and *Jajpurattus*, *Pachypoessa*, and *Phausina* could be hasariines. Tentative molecular results (Maddison et al. 2014) suggest that *Bristowia* and *Cheliceroides* may be the sister group to the other hasariines. They are therefore included here provisionally.

Tribe Chrysillini Simon, 1901
(31 genera; Figs. 90–96)

Simon, 1901: Chrysilleae, Flacilleae
Simon, 1903: Silereae
Petrunkevitch, 1928: Heliophaninae
Roewer, 1954: Augusteae, Chrysilleae, Heliophaninae, Silereae
Prószyński, 1976: Heliophaninae

Remarks.—Formerly known as heliophanines (see Problematic Names, below), the chrysillines are ubiquitous throughout the Old World. They are generally small to medium sized foliage-dwellers with delicate legs, often brightly coloured, including the large genera *Heliophanus* (Wesołowska 1986; Rakov & Logunov 1997) and *Cosmophasis* (Żabka & Waldock 2012). Exceptions to the delicate body form include *Menemerus* and *Pseudicius*, typically bark or rock dwellers, and the relatively large-bodied *Epocilla*. The group has many species with interesting features: some fluoresce (Lim et al. 2007), some reflect and respond to UV light (Lim & Li 2006a, b, 2007; Land et al. 2007; Lim et al. 2008; Li et al. 2008), some are myrmecophages (Pekár & Haddad 2011), *Orsinia* resembles a bug or wasp in reverse (Reiskind 1976), some live in nest aggregations (Jackson 1986b; Maddison 1987), and many have a stridulatory apparatus in both males and females (Maddison 1987). The embolus is fixed to the tegulum.

Monophyly: Many, though not all, chrysillines have a bump on the tegulum about 90° cloekwise from the base of the embolus (left palp ventral view; Maddison 1987; Maddison & Hedin 2003a). A smaller subset has distinctively swollen setal bases on the first femur and a rugose carapace side, suggested to be a stridulatory apparatus (Maddison 1987). Each of these could be a synapomorphy for a subclade of chrysillines, or for the group as a whole with subsequent losses. The Chrysillini is supported as monophyletic by molecular data (Maddison & Hedin 2003a; Bodner & Maddison 2012; Maddison et al. 2014).

Most of the genera included without molecular data can be easily placed here by the classic form of the palp with the tegular bump. The genera *Afraflacilla*, *Heliophanillus*, and *Wesolowskana* all have the chrysilline palp as well as the leg-carapace stridulatory apparatus. Based on the palp and stridulatory apparatus, Ruiz et al. (2007) and Ruiz (2010) place the genera *Kupinka*, *Matagaia*, *Plesiopiuka*, and *Theriella* into the chrysillines, which along with *Helvetia*, *Marchena*, and *Yepoella* are the only New World representatives. Prószyński (2015) suggests that *Tasa* and *Paraheliophanus* are heliophanines and that *Echinussa*, *Hakka* and *Helicius* are chrysillines, placements that are supported by their palps. *Chrysilla* and *Natta* have the classic chrysilline palp, as well as body forms like those of *Siler*, *Mexcala* and *Orsinia*. *Angustea* is included because it appears to be a synonym of *Orsinia* or *Chrysilla*. Based on my examination of the type specimen of *Rooseveltia mutilla* Peckham & Peckham, 1907 in the Museum of Comparative Zoology, the body and markings of *Ogdenia* very closely resemble those of *Siler cupreus* Simon, 1889, though the epigynum has the openings oriented differently (Prószyński 1984b). Prószyński (2015) lists *Jaluiticola hesslei* Roewer, 1944 as a synonym of *Menemerus bivittatus* (Dufour, 1831). The genus *Toticoryx*, listed as Salticinae *incertae sedis*, could be a chrysilline.

Tribe Leptorchestini Simon, 1901
(7 genera; Figs. 103–105)

Simon, 1901: Leptorchesteae
Roewer, 1954: Leptorchesteae

Remarks.—This small but heterogeneous group, unexpected before molecular data (Maddison & Hedin 2003a; Bodner & Maddison 2012; Maddison et al. 2014), includes the pelleninelike *Yllenus* and the ant-like *Leptorchestes*. The only New World lineage is the elongate desert-dwelling *Paramarpissa*. The behavioural ecology of *Yllenus*, by far the largest leptorchestine genus (Logunov & Marusik 2003a) has been studied by Bartos (2002a, b, 2004, 2005, 2007, 2008; Bartos & Szczepko 2012; Bartos et al. 2013).

Monophyly: The only known morphological synapomorphy of this tribe is the loss of retromarginal cheliceral teeth (*Leptorchestes*: Wesołowska & Szeremeta 2001; *Paramarpissa*: Logunov & Cutler 1999; *Yllenus*: Logunov & Marusik 2003a), convergently lost in the Sitticini and some euophryines and aelurillines. Logunov & Marusik (2003a) suggested, without knowledge of the molecular results, that *Paramarpissa* and *Yllenus* may be related, based on the discreteness of a sclerite between the tegulum and the embolus, which they called the radix (Logunov & Cutler 1999, figs. 9-12; Logunov & Marusik 2003a, figs. 58–61). Although this sclerite may be common in salticids (hasariines, Logunov 1999a; freyines, Edwards in

press; euophryines, Zhang & Maddison 2015; see also comments on palps under Methods), its distinctness in *Paramarpissa* and *Ylleuus* is unusual, and thus provides a synapomorphy for these two genera. *Leptorchestes* and related ant-like leptorchestines do not appear to have such a distinct "radix" (Wesołowska & Szeremeta 2001). The group as a whole is well supported by molecular data (Maddison & Hedin 2003a; Bodner & Maddison 2012; Maddison et al. 2014).

Kima has palps very much like *Leptorchestes* (Wesołowska & Szeremeta 2001, figs. 12, 61). Photographs of the type specimen of *Araegeus mimicus* Simon, 1901 taken by Tamás Szűts show a spider whose body and epigynum closely resembles those of *Kima atra* Wesołowska & Russell-Smith, 2000. Wesołowska (2006a) places *Ugaudinella* with *Leptorchestes* because of the ant-like form and the absence of a retromarginal cheliceral tooth.

Tribe Euophryini Simon, 1901
(116 genera; Figs. 106–112)

Peckham, Peckham & Wheeler, 1889: Athamii
Simon, 1901: Bythocroteae, Chalcoscirteae, Coccorchesteae, Diolenieae, Evophrydeae, Saitideae, Sobasineae, Thianieae, Zenodoreae
Simon, 1903: Athameae, Bellieneae, Cytaeae, Emathideae, Laufeieae, Servaeae, Spilargeae
Petrunkevitch, 1928: Coccorchestinae, Cytaeinae, Spilarginae
Roewer, 1954: Coccorchestinae, Cytaeinae, Spilarginae; Athameae, Bellieneae, Bythocroteae, Chalcoscirteae, Cytaeeae, Diolenieae, Ematheae, Euophryeae, Laufeieae, Pensacoleae, Saiteae, Serveae, Sobasineae, Spilargeae, Thianieae, Zenodoreae.
Prószyński, 1976: Euophrydinae
Wanless, 1988: Euophryinae

Remarks.—Although speciose, euophryines are remarkably uniform in genitalia and body form except in tropical Australasia, where atypical forms such as *Dioleuius*, *Sobasina*, *Paraharmochirus*, *Athamas* and *Coccorchestes* exist (Zhang & Maddison 2012b, 2015). Otherwise, the palp typically has a simple spiral embolus (Prószyński 1976; Zhang & Maddison 2015) and the epigynum has windows framed by circular folds that presumably guide the embolus. Elongate or ant-like body forms are rare. The Euophryini is the most cosmopolitan of all taxa ranked as tribes (Zhang & Maddison 2015) with high diversity in all tropics except African, and yet it also has a prominent role in the faunas of colder altitudes and latitudes. The group has recently been studied extensively by Zhang (Zhang & Maddison 2012a, b, c, d, 2013, 2015).

Euophryines are little studied ecologically, though there are many reports of ant feeding (Edwards et al. 1974; Cutler 1980; Jackson & van Olphen 1991, Li et al. 1996, Jackson et al. 1998; Clark et al. 2000; Jackson and Li 2001). Crane (1948) examined the life history and courtship of *Corythalia* in exquisite detail. Perhaps the most widely known euophryines are the peacock spiders (*Maratus*, Fig. 112), whose males have remarkably diverse, complex and colourful ornaments (Żabka 1987b; Otto & Hill 2011a, 2012a, b, 2013a, b, 2014a, b, c; Waldock 2013, 2014) and courtship behaviours (Hill 2009; Otto & Hill 2010, 2011a, b; Girard et al. 2011).

Regarding the decision to use the name "Euophryini" for this group, see the discussion below under "Problematic Names". Prószyński & Deeleman-Reinhold (2013) explain the shift in spelling from "Euophrydinae".

Monophyly: While other groups of salticids have a spiral embolus, its form in most euophryines is distinct from that in most other salticids in being an open spiral facing ventrally, with the axis of the spiral perpendicular to the axis of the palp (Maddison & Hedin 2003a). The loop of the sperm duct inside the tegulum (e.g., Zhang & Maddison 2015, fig. 8) is also partially distinctive, though also seen elsewhere (e.g., some dendryphantines such as *Phanias* and *Rhene*, Maddison 1996, figs. 20, 52). Most species with a long embolus also show distinctive "windows" in the epigynum (Maddison & Hedin 2003a; Zhang & Maddison 2015, fig. 39). Molecular data confirm the group is monophyletic, including the type genera of the Athamii and all of Simon's euophryine groups (Zhang & Maddison 2013; Maddison et al. 2014).

The list of genera here included follows that of Zhang & Maddison (2015) with the following additions. *Baviola*, *Gorgasella*, and *Lauharulla* have been added as per the suggestion of Zhang & Maddison (2015), but not *Lechia* and *Panysinus*, as their placement is too doubtful. *Platypsecas* is included following the tentative suggestion of Ruiz & Brescovit (2005b). *Peusacolops* and *Pseudocorythalia* are added based on figures in their original descriptions, showing euophryine genitalia. The new genera of Richardson (2013) are included except *Ananeon*, which is considered here Salticinae *incertae sedis*, possibly a neonine. *Raralu* is included as it appears to be close to, or synonymous with, *Sobasina*, based on illustrations by Prószyński in Prószyński (2015). *Yacuitella* is included tentatively, as a possible close relative of *Amphidraus*, based on the form of the embolus, cheliceral teeth, and body. The Dominican amber fossil *Peusacolatus* seems clearly euophryine by its palp (Wunderlich 2004). *Udaluella* is not included, though it could be a derived *Tylogonus*, near *T. chiriqui* Galiano, 1994. *Stergusa* might be near *Sobasina*, or it could be a simaethine, and so is listed as Salticinae *incertae sedis*. *Tatari* and *Gambaquezonia*, possibly related, have a spiral embolus, but lack the sperm duct loop typical for euophryines (Berland 1938; Edwards 2009), and so are listed as Salticinae *incertae sedis*. Possible other euophryines among the genera listed as Salticinae *incertae sedis* are *Lechia*, *Leuserattus*, and *Muziris*.

Tribe Salticini Blackwall, 1841
(7 genera; Figs. 113–115)

Blackwall, 1841: Salticidae
Prószyński, 1976: Salticinae

Remarks.—It is remarkable that previous literature has made so little mention of the Salticini or Salticinae, taxa that must exist and contain *Salticus* by traditional nomenclatural rules. While this may be due in part to the past difficulty of finding the close relatives of *Salticus*, it is also due to our failure to correct Simon's placement of *Salticus* in the Marpisseae, until Prószyński (1976) revived the required nominate subfamily. Recent molecular work (Maddison et al. 2014) consistently places *Salticus* as sister group to Maddison et al.'s (2008) "*Philaeus* group". For this reason Maddison et al. (2014) placed the *Philaeus* group within the taxon that is here re-ranked as the Salticini.

The seven genera known to belong to the Salticini occur in Africa, with some extending into Europe and Asia. *Salticus* is the only genus that reaches the New World, with a handful of native species.

Monophyly: There are no known morphological synapomorphies of the tribe. The embolus is fixed, and in all but *Salticus* there is a prominent lobe on the tegulum (Peckham & Peckham 1903, plate XXII fig. 4A [*Pignus*]; Andreeva et al. 1981, figs. 1, 6 [*Mogrus*]; Prószyński 1984a, p. 149 [*Tusitala*], 1992b, fig. 7 [*Carrhotus*], 2003, figs. 403 [*Mogrus*], 503 [*Philaeus*]). Prószyński (2003) suggested that *Mogrus* and *Philaeus* are related.

The claimed type locality for *Diagondas viridiaureus* Simon, 1902, Brazil, is almost certainly a result of mislabelling (as for *Thiratoscirtus patagonicus* Simon, 1886: Tamás Szűts, pers. comm; Wesołowska & Russell-Smith 2011). No other specimens of *Diagondas* have been reported from South America. *D. viridiaureus* is very close to, or a senior synonym of, *Carrhotus malayanus* Prószyński, 1992, from southest Asia (compare Prószyński 1992b: figs. 1–4 to Galiano 1963a: plate XV figs. 11–13; also, a male specimen recently collected by me in Borneo is a nearly perfect match to Galiano's drawings). *Diagondas* Simon, 1902 is therefore considered a junior synonym of *Carrhotus* Thorell, 1891, **NEW SYNONOMY**).

Tribe Aelurillini Simon, 1901
(51 genera; Figs. 116–124)

Simon, 1901: Aelurilleae
Maddison, Bodner & Needham, 2008: Aelurilloida

Remarks.—This group of more than 500 species, called the Aelurilloida by Maddison et al. (2008), contains the distinctive aelurillines along with the Neotropical freyines and Afrotropical thiratoscirtines.

Monophyly: Although freyines and thiratoscirtines resemble each other in body form and markings, there are no known morphological synapomorphies to link them to each other or the somewhat more distinctive Aelurillina. The group is well supported by molecular data (Maddison et al. 2014).

Subtribe Aelurillina Simon, 1901
(11 genera; Figs. 116–118)

Simon, 1901: Aelurilleae
Roewer, 1954: Aelurilleae
Prószyński, 1976: Aelurillinae

Remarks.—Although speciose, this ground-dwelling group is rather uniform in appearance, with a slightly narrowed carapace and stout legs. *Langelurillus* and *Phanuelus* are exceptions (Fig. 116; Caleb et al. 2015, figs. 26–37), being smaller and more compact, resembling small *Habrocestum*, *Naphrys* or *Ailluticus*. Among the best-known genera are *Aelurillus* and *Phlegra* (Azarkina 2002, 2003, 2004, 2006). Only a single species of this Afro-Eurasian group has reached the New World, *Phlegra hentzi* (Marx, 1890). Several aelurilline species are reported to live with or eat termites (Wesołowska & Cumming 2002; Wesołowska 2007; Wesołowska & Haddad 2009). Some *Langelurillus* and *Phanuelus* lack a tooth on the cheliceral retromargin (Wesołowska & Russell-Smith 2000; Caleb et al. 2015).

Monophyly: The palp has a distinctive appearance, with the tegulum oval, distally extended as a shield hiding the embolus, and proximally pointed (e.g., Logunov 1996a, fig. 32; Maddison 1996, fig. 18; Azarkina 2002, fig. 2). Logunov (1996a) proposes a pocket on the cymbium as a synapomorphy of the group (Logunov 1996a, figs. 2–4, 32). The embolus is spiral in many speeies, and separated from the tegulum by a hematodocha (e.g., Logunov, 1996b, figs. 1–5; Maddison 1996, fig. 18; Azarkina 2002, figs. 5, 6). The thorax is often marked by longitudinal bands of white or pale scales at or just medial to the PLE (Fig. 118).

Subtribe Freyina Edwards, 2015
(26 genera; Figs. 119–121)

Edwards, 2015: Freyinae

Remarks.—A Neotropical group of medium- to large-bodied salticids typically having simple palps with a fixed embolus, resembling plexippines to some extent. It is the smallest and most morphologically uniform of the four major groups of Neotropical salticines (the other three being the Amycoida, Marpissoida and Euophryini). The group was a focus of study by Galiano (1961, 1968a, 1970, 1978, 1979a, b, c, 1981a, b, c, 1982, 1983, 1984, 1994, 1995, 2000, 2001). Edwards (in press) reviews the group comprehensively and describes several new genera.

Monophyly: Edwards (in press) notes there are no known strongly diagnostic synapomorphies for the group, but suggests two traits that could be synapomorphies, though not universally present: (1) subdistal and subproximal prolateral leg tibial macrosetae, and (2) a very thick basal division of the tegulum with a groove in its distal side. Edwards (in press) describes freyines as often having a conductor that accompanies the embolus, an anterior eye row about 5% wider than the posterior, and conspicuous setal tufts on the basal leg segments. The male palp has a strong and distinct cleft cutting diagonally across the front face of the bulb, and often bears a proximal tegular lobe as in euophryines (Galiano 1979b, figs. 36–43, 1979c, figs. 5, 6, 1994, figs. 7–10, 2001, figs. 14, 17). The thorax is often marked by one medial and two lateral longitudinal bands of white or pale scales below the PLE (Figs. 119, 120), more or less the negative of the aelurilline pattern. However, these features are not perfectly diagnostic. Even still, in the context of the Neotropics, freyines are usually easy to recognize, lacking the unusual body forms of amycoids, the angular carapaces and freely movable embolus of the Marpissoida, and the spiral embolus of euophryines. If not for geographical distribution, they would be difficult to distinguish from thiratoscirtines. Nonetheless, when such Neotropical species are accumulated, they are found to hold together by molecular data (Maddison & Hedin 2003a; Bodner & Maddison 2012).

Among the genera listed as Salticinae *incertae sedis*, *Hisukattus* could be a freyine.

Subtribe Thiratoscirtina Bodner & Maddison, 2012
(14 genera; Figs. 122–124)

Bodner & Maddison, 2012: Thiratoscirtinae

Remarks.—A group endemic to Africa, concentrated in the wetter tropics of Central and West Africa. In Gabon at least,

they are the most speciose and common group of salticids within the forests, while other groups such as plexippines and chrysillines dominate outside the forests (Bodner & Maddison 2012). Thiratoscirtines are remarkable for the large number of species that can be found on leaf litter sympatrically (Jocqué & Szűts 2001; Bodner & Maddison 2012). Most recent work on the group has been due to Szűts, Wesołowska and colleagues (Szűts & Jocqué 2001; Rollard & Wesołowska 2002; Szűts & Scharff 2005; Szűts & Rollard 2007; Wesołowska & Russell-Smith 2011; Weso?owska & Edwards 2012; Wesołowska & Haddad 2013).

Monophyly: Bodner & Maddison (2008) diagnosed the thiratoscirtines with molecular data, demonstrating their monophyly with data from five genes. The epigynum of thiratoscirtines often has an abrupt, deep and broad central depression, and often has a posterior tongue-like extension (Szűts & Jocqué 2001, fig. 4; Szűts & Rollard 2007, fig. 1C, Wesołowska & Russell-Smith 2011, figs. 171, 191, 199). The palps are almost always unusual, but seemingly in different ways. What might unite their atypicality has not been articulated. The embolus is usually fixed, but sometimes apparently not (e.g., Maddison et al. 2008, figs. 4, 5). When fixed, the embolus often appears to wander away from the tegulum in strange directions — e.g., *Pochyta fastibilis* Simon, 1903, *Thiratoscirtus capito* Simon, 1903. Indeed, this dissociation of the embolus from a typical path is what leads to the placement here of *Ajaraneola*, *Cembalea*, *Nimbarus*, and *Ureta*. This is tentative, however, as some Salticini (e.g., *Pignus*, Peckham & Peckham 1903, plate XXII fig. 4A) also have a loosely directed embolus. In some thiratoscirtine species, it appears that the subtegulum and hematodocha are unusally exposed (e.g., *Pochyta pamosa* Simon, 1903, Maddison et al. 2008, fig. 5). It may be that some functional shift in the bulb has released the thiratoscirtine palp to evolve in patterns not normally seen in salticids. Despite this lack of morphological clarity, when the non-plexippine salticines with generally freyine-like bodies in central African forests are studied, the molecular data clearly put them together as a group (Bodner & Maddison 2012).

Graneuca is placed here by its epigynum with posterior tongue; *Lanotella* by its palp closely resembing *Pochyta pulchra* (Thorell, 1899). Possible thiratoscirtines among the genera listed as Salticinae *incertae sedis* are *Hasariella* and *Maltecora*.

Tribe Plexippini Simon, 1901
(47 genera; Figs. 125–136)

Simon, 1901: Plexippeae
Maddison & Hedin, 2003a: Plexippoida
See further synonyms under subgroups.

Remarks.—This large group (nearly 800 species), first recognized by Maddison & Hedin (2003a) as the Plexippoida, is second among tribes only to the Euophryini in number of species, though that may reflect considerable attention by arachnologists, as they are often large, commonly collected by beating, and diverse in long-studied Eurasia. Compared to such groups as astioids or amycoids, they tend to be rather conservative in body form, with the elongate (e.g., *Telamonia*), beetle-like (*Hermotimus*), or ant-like (*Eburneana*) body forms being only weakly so. However, it should be remembered that they are merely a subgroup of the Saltafresia, and likely considerably younger than the astioids or amycoids (Fig. 1). The Plexippini includes two subgroups, the Plexippina and the Harmochirina.

The embolus is fixed to the tegulum, which is usually circular or slightly oval in shape.

Monophyly: Two synapomorphies, a modified serrula on the male endite (Maddison & Hedin 2003a, fig. 7) and a lobe on the tegulum just clockwise (left palp, ventral view) from the base of the embolus (Prószyński 1987, p. 80; Marusik & Logunov 1998, figs. 1, 4; Wesołowska & van Harten 1994, fig. 151), were originally thought by Maddison (1988, 1996) to delimit what is here called the subtribe Plexippina, but insofar as they apply also to *Harmochirus* and close relatives, they are better considered synapomorphies of the Plexippini (see Maddison & Hedin 2003a), secondarily lost in the pellenine harmochirines. The Plexippini is strongly supported by molecular data (Maddison & Hedin 2003a; Bodner & Maddison 2012; Maddison et al. 2014).

Vatovia, assigned to Salticinae *incertae sedis*, could be in the Plexippini judging by figures in Caporiacco's (1940) original description.

Subtribe Plexippina Simon, 1901
(32 genera; Figs. 125–130)

Simon, 1901: Plexippeae, Hylleae, Thyeneae
Simon, 1903: Hermotimeae
Petrunkevitch, 1928: Plexippinae, Hyllinae, Thyeninae
Roewer, 1954: Plexippinae, Plexippeae, Barypheae, Hyllinae, Hylleae, Thyeninae, Thyeneae
Prószyński, 1976: Plexippinae, Hyllinae
Maddison, 1996: Plexippinae

Remarks.—This Old World group has only two native species in the New World, both *Evarcha*. It is approximately equivalent to Maddison's (1988, 1996) concept of the Plexippinae. Most are relatively large salticids with robust legs, including the familiar cosmotropical *Plexippus paykulli* (Audouin, 1826). Their conservatism in body and genitalia makes generic limits problematical, with genera such as *Evarcha*, *Pancorius* and *Hyllus* difficult to distinguish except perhaps by size.

Monophyly: Although there are no known synapomorphies of this group, they are generally easy to recognize by the large size, usually round palp bulb, simple fixed embolus, and robust legs. Many species have tufts of setae beneath the PMEs that project laterally and forward (Żabka 1985, fig. 217; Wesołowska & van Harten 1994, figs. 150, 152). The molecular data for monophyly are strong (Bodner & Maddison 2012). The guide of the epigynum is often shifted anteriorly from the margin, as in the related harmochirines, but often split into two lateral pockets (e.g., *Evarcha*, *Hyllus*, *Pancorius*, *Yaginumella*).

Given their simple palps and generalized (though usually robust) body form, the limits of this group have been unsettled. Prószyński (1984b) was the first to recognize that species formerly placed in *Viciria* pertain to two very different groups, some belonging with the plexippine *Telamonia*, others remaining in *Viciria*, which is now placed in the Astioida.

Pseudamycus and *Artabrus* are included on the basis of an epigynum with a divided guide pocket. In *Pseudamycus*, it is divided into two separate lateral pockets as in *Evarcha* and *Pancorius*. *Taivala invisitata* Peckham & Peckham, 1907 (types in Museum of Comparative Zoology, examined) is close to, or a synonym of, *Pancorius dentichelis* Simon, 1899. As noted by Prószyński & Deeleman-Reinhold (2013), *Vailimia* is a plexippine (type specimen of *Vailima masinei* Peckham & Peckham, 1907 in Museum of Comparative Zoology, examined). It is close to, and possibly a synonym of, *Pancorius*. Tamás Szűts (pers. comm.) was kind enough to supply photographs of the type specimen of *Pachyonomastus kittenbergeri* Capporiacco, 1947, by which it appears to be very similar to *Thyene semiargentea* (Simon, 1884). *Afrobeata* is placed here tentatively on the basis of the lateral pockets of the epigynum (Prószyński 1987), and the eye tufts reminiscent of *Hyllus* and *Thyene* (photograph of type supplied by Tamás Szűts, pers. comm.). *Dasycyptus* has an *Evarcha*-like palp (Prószyński 1987), but is poorly studied. Szűts & Scharff (2005) indicates that *Encymachus* "is most similar to the African *Hyllus*". Prószyński (2015) indicates that *Pseudoplexippus unicus* Caporiacco, 1947 is a synonym of *Plexippus petersi* (Karsch, 1878). *Paraplexippus* is likely a synonym of *Plexippus*, based on Franganillo's (1930) figures and comments. The robust body and eye tufts suggest that *Parajotus* belongs here, but this must be considered highly tentative. *Pharacocerus* resembles *Pancorius* in palp, robust body, and eye tubercles, but it may belong elsewhere. Possible plexippines among the genera listed as Salticinae *incertae sedis* are *Bokokius*, *Maltecora*, *Tamigalesus*, and *Yogetor*.

Subtribe Harmochirina Simon, 1903
(15 genera; Figs. 131–136)

Simon, 1903: Harmochireae
Petrunkevitch, 1928: Pelleninae
Roewer, 1954: Harmochireae, Pelleninae
Prószyński, 1976: Pelleninae

Remarks.—This subtribe includes two primary subgroups, the harmochirines *sensu stricto* (e.g., *Bianor*, *Harmochirus*, *Sibianor*) and the pellenines (e.g., *Pellenes*, *Habronattus*, *Havaika*, *Neaetha*). The pellenines are well known for the Holarctic *Pellenes* and the primarily-Nearctic *Habronattus* (Griswold 1987; Maddison & Hedin 2003b), the latter remarkable for its complex and colourful courtship traits (Peckham & Peckham 1889, 1890; Maddison & Stratton 1988; Richman & Cutler 1998; Maddison & McMahon 2000; Elias et al. 2003, 2005, 2006a, b, 2012; Hebets & Maddison 2005; Taylor & McGraw 2013; Taylor et al. 2014a), visual system (Zurek et al. 2015) and chromosomes (Maddison 1982; Maddison & Leduc-Robert 2013). The pellenines are athletic salticids, typically dwelling on open sunny ground like aelurillines and sitticines. In contrast, the harmochirines *sensu stricto* are usually compact, often beetle-like, with more delicate walking legs.

For explanation of the decision to use "Harmochirina" rather than "Pellenina", see "Problematic Names", below.

Monophyly: The epigynal notch receiving the male's tibial apophysis has moved forward on the epigynum, yielding a more or less conical pocket flanked by two crescent shaped openings (e.g., Griswold 1987, figs. 108–149; Prószyński 2008, figs. 69–84; Logunov 2009, figs. 13, 31, 40). Although this has been obscured secondarily in some *Pellenes* and in *Habronattus paratus* (Peckham & Peckham, 1896), it is a synapomorphy of the group. Two of the three subgroups, the harmochirines *sensu stricto* and the pellenines, are strongly united by molecular data (Bodner & Maddison 2012; Maddison et al. 2014). The third subgroup, the ant-like *Eburneana*, is ambiguously linked to the first two by molecular data (Maddison et al. 2014), but can be placed in the group by the epigynal pocket.

Iranattus (Prószyński 1992a) and *Monomotapa* (Wesołowska 2000) share with *Pellolessertia* (Szűts & Scharff 2005) a robust carapace with PLE on tubercles, and with *Pellolessertia* and *Neaetha* extremely long third legs. (Prószyński 1992a says the long legs of *Iranattus* are the fourth pair, but his figures 35 and 36 appear to show they are the third pair.) Their palps are consistent with those of pellenines, and have an unusual cymbial extension like that seen in some *Pellenes* (e.g., *Pellenes bonus* Logunov, Marusik & Rakov, 1999), although similar extensions are seen elsewhere (e.g., the simaethine *Irura*). These features indicate a placement of *Iranattus* and *Monomotapa* with the pellenines, as *Pellolessertia* and *Neaetha* have typical harmochirine genitalia in both males and females. Denis's (1947) figure of the epigynum of *Paraneaetha* suggests it has the guide and atria typical of harmochirines. Thus, the pellenines provisionally include *Pellenes*, *Habronattus*, *Havaika*, *Neaetha*, *Iranattus*, *Monomotapa*, *Pellolessertia*, and *Paraneaetha*; the harmochirines *sensu stricto* include *Harmochirus*, *Bianor*, *Sibianor*, *Napoca*, and *Microbianor*; the eburneanines include only *Eburneana*. Whether *Modunda* is a harmochirine *sensu stricto* or a pellenine is unclear.

PROBLEMATIC NAMES

With this review of salticid classification, several available suprageneric names have been found to be older than commonly used names. These are:

- Harmochireae Simon, 1903 is older than Pelleninae Petrunkevitch, 1928
- Chrysilleae Simon, 1901 is older than Heliophaninae Petrunkevitch, 1928
- Athamii Peckham, Peckham & Wheeler, 1889 is older than Euophrydeae Simon, 1901
- Cocalodeae, Cyrbeae, and Cocaleae Simon, 1901 are older than Spartaeinae Wanless, 1984.

In each case, the younger name has been used as a subfamily, while the older name was described as a taxon called simply a "group", with unclear rank in the modern scheme. Through much of the 20th century, there was a tradition of describing new subfamilies without regard to older "group" names (e.g., Petrunkevitch 1928; Wanless 1984) as if the latter were not coordinate with subfamily names for priority. For example, Simon (1901) placed the nominate genus *Salticus* in the group Marpisseae, and Roewer (1954) did likewise for several subfamilies (e.g., *Heliophanus* in the group Chrysilleae within the subfamily Heliophaninae). Bonnet (1955–1959), normally an activist in correcting errors, lists without comment synonymies showing older group names as synonyms beneath younger subfamily names. This treatment suggests that early 20th century

authors viewed "group" names as following rather different rules than subfamilies, as if they were informal and acceptably ignored. However, more recently, arachnologists have treated these group names as within the ranks of the family group, available as subfamilies or at other ranks. This shift in interpretation challenges us to consider older names that were long disregarded. The taxonomic rank of these "groups" could be considered ambiguous, but they have been considered below the rank of subfamily (e.g., Roewer 1954), as if equivalent to tribes.

While article 35.5 of the current code (ICZN 1999) might have permitted us to retain the younger higher-ranked subfamily names, this article would no longer apply once their rank is reduced to tribe, which I do for all but Spartaeinae.

The simplest case is perhaps Harmochireae/Pelleninae. Insofar as both have continued to be used (e.g., Logunov 2009), but not commonly in the literature, it is best to give way to priority, with subtribe Harmochirina taking precedence over the alternative choice Pellenina. However, the pellenines are still recognized, informally, as a subgroup of the Harmochirina.

In the other three cases, a strict application of the Code would likewise support older and more-or-less forgotten names to displace names currently in common use. Of these, the displacement of "Heliophaninae" is the least disruptive, as its uses in the literature are not extensive. While the group's genera are among the most conspicuous salticids throughout the Old World, their collective labelling as heliophanines is not so conspicuous in the literature. Therefore, I use Chrysillini for the group, treating Heliophaninae as a junior synonym.

However, "Euophryinae" cannot be so painlessly set aside. Because of strong prevailing use in salticid systematics, I use Euophryini in preference to the older Athamii. Among the groups heretofore recognized as subfamilies, the Euophryinae is the largest and most widespread, with over 1000 species and 100 genera on all continents except Antarctica, from the tropics to cold temperate habitats (Zhang & Maddison 2015). Our current concept of this group dates to Prószyński's (1976) landmark paper. While it is easy to recognize a salticid as belonging to the group, it has been difficult to distinguish genera (Zhang & Maddison 2015). Thus, for the last 40 years we have often spoken of "euophryines" and identified specimens as "euophryine", without referring to the genus, both in the literature and in our informal parlance. The names "Euophryinae" and "euophryine" have come to be key parts of the vocabulary of salticid systematics (e.g., Prószyński 1976, 1983a, 2003, 2009b; Prószyński & Żabka 1980; Żabka 1980b, 2012; Griswold 1987; Logunov 1992, 1998; Maddison 1996; Wesołowska & Russell-Smith 2000; Wesołowska 2001, 2012; Żabka & Pollard 2002b, c; Edwards 2003a, b, 2004, 2009; Logunov & Kronestedt 2003; Maddison & Hedin 2003a; Benjamin 2004; Edwards et al. 2005; Ruiz & Brescovit 2005b, 2008a, b; Arnedo & Gillespie 2006; Andriamalala 2007; Ruiz et al. 2007; Su et al. 2007; Logunov & Azarkina 2008b; Azarkina 2009; Hill 2009, 2012; Otto & Hill 2011a, 2012a, b, 2013a, b, 2014a, b, c; Prószyński & Deeleman-Rheinhold 2012, 2013; Zhang & Maddison 2012a, b, c, d, 2013, 2015; Azarkina & Foord 2013; Edwards & Ruiz 2013; Richardson 2013; Ruiz 2011, 2013b; Waldock 2013, 2014; Wesołowska & Haddad 2013, 2014; Wesołowska et al. 2014). In contrast, the older name Athamii (or Athameae) has been used rarely (Simon 1903; Roewer 1954; Galiano 1976b; Szűts 2003b), though enough to prevent its being considered a *nomen oblitum*. The use of Athamii/Athameae has been restricted to the rarely collected and little studied nominate genus *Athamas* of Australasia and Pacific Islands (Jendrzejewska 1995). Prószyński & Deeleman-Rheinhold (2013) recognized that *Athamas* is a euophryine, but did not address the priority of names, possibly because the Athamii/Athameae has been misattributed to Simon (e.g., Jendrzejewska 1995, Szűts 2003b). Because of the importance of the name "Euophryinae" to salticid systematics, I will use Euophryini as the name of the tribe.

The case of Spartaeinae is more complex, but I use that familiar name instead of the alternatives because of its widespread use in literature on salticid behaviour and systematics, cited below. When Wanless (1984a) named the subfamily Spartaeinae because of homonymy of the former Boethinae's type genus, he ignored the availability of Simon's older group names Cocalodeae, Cyrbeae, and Cocaleae, possibly because he did not consider them as coordinate with family-group names. Noticing Wanless's error, Wunderlich (2004) proposed Cocalodinae instead. At first glance, it would appear that the Code rules out Wunderlich's change, with article 35.5 preventing Spartaeinae's replacement by a lower ranked name (Cocalodeae). However, that article specifies that the older name be in use (despite this requirement seeming against the intent of the article), and Cocalodeae arguably was not in use. Thus, a direct reading of the Code leads us to the subfamily name as the Cocalodinae.

What would be the name of the tribe excluding *Codalodes* but including *Cyrba*, *Cocalus*, and *Spartaeus* (Table 2)? Besides Spartaeini, there are two competing names for this tribe, based on Cyrbeae or Cocaleae, of which I would choose Cyrbeae because the type genus is considerably more widespread. Here again, article 35.5 cannot protect the Spartaeini, for any of three reasons: (1) Spartaeini as a tribe does not outrank Simon's group, if we treat groups as of tribal rank; (2) "Cyrbeae" has not been in use; (3) Cyrbeae does not represent a distinct taxon from the Spartaeini even at the lowest level, as *Cyrba* and *Spartaeus* have long been placed together even at the finest level (here, the same subtribe). This last requirement, for distinctness at the lowest level, I interpret as the spirit of the Code, implied by the example given in the Code for article 35.5. Even if 35.5 would protect the subfamily name Spartaeinae, the lower levels of tribe and subtribe would not be so protected, leading to the inconsistency that *Spartaeus* and *Cyrba* would find themselves together within the subtribe Cyrbina, tribe Cyrbini, subfamily Spartaeinae.

According to the cited articles of the Code and the principle of priority, therefore, the appropriate names for groups containing *Cyrba* and *Spartaeus* would be Cocalodinae: Cyrbini: Cyrbina, accepting Wunderlich (2004) as first revisor. However, there is a compelling argument to maintain current usage for stability. There is much work anchored to the name Spartaeinae in the literature of salticid behaviour (Blest 1984, 1987; Jackson & Hallas 1986b; Blest et al. 1990; Jackson 1990a, b, c, d, 2000, 2002; Jackson & Pollard 1990, 1996; Jackson & Li 1998; Harland et al. 1999; Bartos 2002b; Li 2000; Cerveira et al. 2003; Guseinov et al. 2004; Nelson & Jackson 2009a; Cerveira & Jackson 2011; Hu et al. 2012; Nelson et al. 2012; Cross & Jackson 2015) and systematics (Wanless 1984a,

b, 1985, 1987; Bohdanowicz & Prószyński 1987; Griswold 1987; Davies & Żabka 1989; Rodrigo & Jackson 1992; Wijesinghe 1992, 1994; Maddison 1996, 2006, 2009; Żabka & Kovac 1996; Galiano 1998, 2000; Logunov 1998; Żabka 1999; Szűts & Azarkina 2002; Deeleman-Reinhold & Floren 2003; Maddison & Hedin 2003a; Prószyński 2003; Edwards 2004; Zhang & Li 2005; Maddison & Needham 2006; Maddison et al. 2007, 2008, 2014; Su et al. 2007; Logunov & Azarkina 2008a; Wesołowska & Haddad 2009, 2013; Azarkina & Logunov 2010; Benjamin 2010; Hill 2012; Prószyński & Deeleman-Reinhold 2012; Ruiz & Maddison 2012; Ruiz 2013a; Zhang & Maddison 2013, Zhou & Li 2013a; Logunov & Marusik 2014; Ramírez 2014; Patoleta & Żabka 2015). To avoid disconnecting that literature from the classification, I use Spartaeinae: Spartaeini: Spartaeina.

EVOLUTION AND BIOGEOGRAPHY

While the arrangement is presented here as a classification, it also represents the first time that explicitly phylogenetic relationships have been proposed for all (or most) genera of salticids. Such a classification has two roles. First, by placing together related genera, it promotes species discovery and taxonomic work, by assembling together those genera that might hold species relevant for a study, facilitating the search for already-described species. Second, it promotes exploration of evolutionary patterns in salticids.

The age and biogeography of salticid radiations.—Major clades of salticids are mostly restricted to a single continental area (Maddison & Hedin 2003a; Bodner & Maddison 2012). In the speciose Salticinae, the Amycoida are primarily Neotropical, the Astioida primarily Australasian, the Marpissoida primarily in the Americas (especially Central and North America), and the Saltafresia (with the exception of the euophryines and freyines) primarily Afro-Eurasian. The Spartaeinae is similarly divided, with the Americas, Afro-Eurasia and Australasia occupied by the lapsiines, spartaeines, and cocalodines respectively. This pattern suggests that each major group diversified mostly in isolation from the others, after the continents were fully isolated about 35 million years ago (Maddison & Hedin 2003a; Bodner & Maddison 2012). This timing of salticid radiations is supported by dating of divergence times using molecular data and fossils (Bodner & Maddison 2012; Zhang & Maddison 2013). Even before molecular data clarified relationships, Żabka (1990b, 2000) and Żabka et al. (2002) pointed out the lack of any trace of a Gondwanan salticid fauna.

At present, each continental area has its own distinct fauna consisting primarily of a few groups — e.g., Amycoida, Dendryphantini, Freyina, and Euophryini in the Neotropics, contrasted against Euophryini, Plexippina, Chrysillini, Spartaeina, and Astioida in the Asian tropics — but the faunas may have been even more distinct in the past. One is tempted to imagine a time in the mid-Cenozoic during which South America, North America, Afro-Eurasia and Australia each had its own major isolated radiation (the amycoids, marpissoids, saltafresians and astioids respectively).

It should be realized, however, that the relationships presented here are not entirely independent evidence for isolated radiations. The strength of this geographical pattern has likely influenced my assessments of the relationships of some poorly studied genera, such that I may have been more likely to predict that an Australian salticine species with fixed embolus is an astioid rather than a marpissine, for example.

Salticid eyes and vision.—Many studies have explored various aspects of salticid vision: anatomy (Scheuring 1914; Land 1969a, 1985; Eakin & Brandenburger 1971; Homann 1971; Hill 1975; Oberdorfer 1977; Blest & Maples 1979; Williams & McIntyre 1980; Blest 1983, 1984, 1985, 1987; Blest & Price 1984; Blest & Sigmund 1984, 1985; Blest & Carter 1987; Blest et al. 1988; Blest et al. 1990; Hu et al. 2012; Zurek et al. 2015), neurophysiology and cognition (Land 1969b; Hill 1975; Duelli 1978; Hardie & Duelli 1978; Sivertson 1985; Baker et al. 2009; Spano et al. 2012; Zurek & Nelson 2012a, b; Nagata et al. 2012; Menda et al. 2014), opsins and colour sensitivity (Devoe 1975; Yamashita and Tateda 1976; Blest et al. 1981; Peaslee & Wilson 1989; Nakamura & Yamashita 2000; Lim & Li 2006a; VanderSal & Hebets 2007; Koyanagi et al. 2008; Nagata et al. 2010; Terakita & Nagata 2014; Taylor et al. 2014b), and behavioural responses (Drees 1952; Land 1972; Giulo 1979; Zurek et al. 2010; Bednarski et al. 2012; Dolev & Nelson 2014). Their visual systems have even inspired robotic camera systems (Tonet et al. 2008).

With this phylogenetic arrangement of salticids, we are now in a position to interpret evolutionary patterns in visual system diversity. Diversity is expected, given that the family is comparable, in species diversity and age, to groups such as the eutherian Mammalia or the passerine birds. Indeed, the Salticinae (and possibly the hisponines) differ distinctly from the other salticids in having the AME retina boomerang-shaped and the AME rhabdomeres rotated to eliminate suture lines (Blest et al. 1990). However, we are hampered in exploring evolutionary patterns by a lack of data from diverse taxa. For instance, the ultrastructure of the AME has been studied in the Lyssomaninae, Asemoneinae, Spartaeinae (Spartaeina, Cocalodini); Amycoida (Gophoini, Sitticini, Scopocirini, Simonellini, Amycini); Astioida (Myrmarachnini, Astiini, Viciriini); Marpissoida (Dendryphantina, Itatina), and Saltafresia (Euophryini, Freyina), as compiled by Blest et al. (1990). The Plexippina is not included in this list, as the reported *Plexippus validus* Urquhart, 1893 is the euophryine *Servaea incana* (Karsch, 1878). Thus, there is scant coverage of the most diverse of the major clades, the Saltafresia. Nonetheless, we can conclude that there is convergence: the amycoids, astioids, and saltafresians each contain species with different conditions in whether the AME Layer 1 receptive segments are continuous or well separated (see Blest et al. 1990). Obtaining more data on anatomy and physiology of diverse salticids will be vital to understand how and why their remarkable eyesight has evolved.

Salticids that look like ants, beetles, and other things.—Ant-like body forms and behaviour in salticids are well known (Peckham & Peckham 1892; Cushing 1997; Ceccarelli 2008; Huang et al. 2011; Nelson 2011; Uma et al. 2013; Pekár 2014), and many of the spiders bearing them have special behaviours that enhance their resemblanee to ants (Reiskind, 1972). The degree of resemblance, to human eyes, varies from mild (e.g., *Tutelina*, *Mexcala*) to highly convincing, with strangely constricted body parts and well-placed markings (e.g., *Synemosyna*, *Myrmarachne*).

A long-standing question is how many independent origins there are of ant-like bodies and behaviour in salticids

(Jackowska & Prószyński 1975). Pekár (2014) concludes that strongly ant-like bodies evolved in six salticid lineages. The more complete picture of salticid relationships presented here indicates that strong ant (or wasp) mimicry has evolved at least 12 or 13 times in salticids. The following list shows the scattered distribution of ant-like bodies:

- Cocalodini: *Depreissia* (Weso?owska 1997; Deeleman-Reinhold & Floren 2003)
- Amycoida
  - Thiodinini: *Atomosphyrus* (see Ruiz & Maddison in press)
  - Sarindini: *Sarinda*, *Zuniga*, etc. (Figs. 47, 48)
  - Simonellini: *Synemosyna*, *Fluda*, *Erica* (Figs. 41–43, 46)
- Salticoida
  - Agoriini: *Agorius*, *Synagelides* (Figs. 56, 57)
  - Astioida: *Myrmarachne*, etc. (Figs. 78, 79)
  - Marpissoida
    - Ballini: *Marengo*, *Leikung*, etc. (Fig. 61)
    - Dendryphantini
      - Synagelina: *Synageles*, *Peckhania*, etc. (Figs. 68, 69)
      - Dendryphantina: *Bellota*, etc. (Fig. 74)
  - Saltafresia
    - Chrysillini: *Yepoella* (Fig. 95)
    - Leptorchestini: *Leptorchestes*, *Kima*, etc. (Fig. 105)
    - Euophryini: *Sobasina*, *Paraharmochirus* (Zhang & Maddison 2015, figs. 836–841)
    - Plexippini: *Eburneana* (Fig. 133)

In this list are at least 12 independent evolutionary origins, because, in each case, the ant-like species are embedded within clades of non-ant-like species, or have close relatives that are not ant-like. The agoriines are probably a 13th independent origin. However, given the uncertainty in their phylogenetic placement, we cannot yet rule out their sharing an origin of ant-like bodies with some other salticoids. Another caveat is that the selective force for these body forms may not have always been ant mimicry. For example, Christa Deeleman-Reinhold (pers. comm.) suggests that the ant-like *Depreissia* may have been selected for resemblance to polistine wasps. Nonetheless, the phylogenetic distribution of ant-like bodies suggests an answer to the question posed by Jackowska & Prószyński (1975): a strongly ant-like form has neither evolved once, forming a single clade of ant-like salticids, nor in every species independently. Rather, it has evolved a handful of times, with some origins leading to a large diversification of many ant-like species (myrmarachnines, simonellines), and others only a few.

Other salticids are round, dark and shiny, strongly resembling beetles. A striking beetle-like appearance has evolved at least eight times in salticids: in the Amycoida (*Cylistella*, Figs. 44, 45), the Astioida (*Sinaetha* and others, Fig. 88), the Ballini (*Pachyballus*, Fig. 60), the Dendryphantini (*Sassacus, Rhene, Rhetenor*, Fig. 76), and the Euophryini (*Coccorchestes*, Fig. 109).

A surprising pattern is that in at least four of these beetle-like lineages, close relatives of the beetle-like forms are ant-like (*Cylistella*/*Synemosyna*, *Pachyballus*/*Marengo*, *Sassacus*/*Bellota* and *Coccorchestes*/*Sobasina*). A somewhat less-striking beetle-like form (*Attidops*) has the ant-like *Synageles* and *Peckhania* as close relatives.

Orsinia (Chrysillini) has been reported as resembling a backwards insect, with the spinnerets like the insect's mouthparts (Fig. 90; Reiskind 1976). This is indeed convincing, and is replicated in some *Asemonea* (Asemoneinae; Fig. 4), and in different form in *Abracadabrella* (Astioida?).

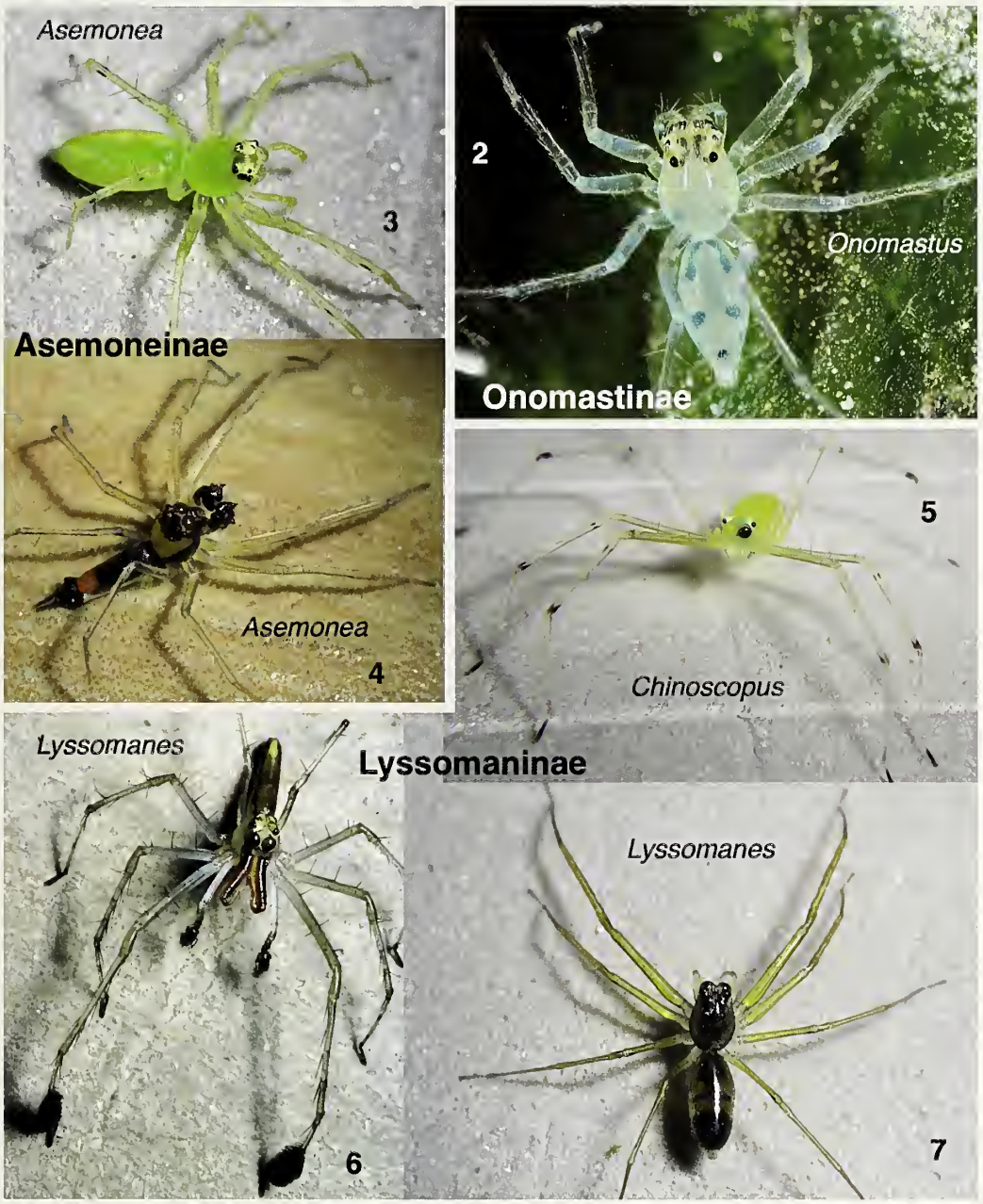
PRIORITIES FOR FUTURE STUDY

Acquiring molecular data from many genes is the priority for resolving salticid relationships with greater clarity. However, for many salticid genera, finding more certain placement will require a better understanding of struetures of the body and genitalia. While standard illustrations of palps and epigyna (both external and internal) are sufficient for species identification, they have not yet yielded many clear synapomorphies for groups. For that, we need to observe structures at much higher resolution than is usually done; a sketch at 80X magnification is not likely enough for phylogenetic work. We also need to go beyond genitalia to fine structures of the whole body. It is also critical that the morphological data be analyzed cladistically, seeking and explaining synapomorphies clearly and explicitly.

However, our greatest challenge is the size of the group compared to the number of active workers. The great bulk of work this century has been led by just a few people in each major continental area: Prószyński, Logunov, Marusik, Peng, and Azarkina for Eurasia; Wesołowska, Russell-Smith, Haddad, and van Harten for Africa and adjacent areas; Żabka for Australasia; Ruiz for the Americas; Maddison and Zhang for multiple areas. While each of the above has participated in describing at least 50 new species, the pace is far too slow given the family's size and the continuing loss of habitat. The need to recruit more workers is especially acute in the Neotropics, South Asia, Southeast Asia, and Australasia. Perhaps, as the family becomes better described and organized, young arachnologists will find it a less daunting vocation.

ACKNOWLEDGMENTS

I thank David Maddison for sharing his wisdom, always, on systematics. I am grateful to G.B. Edwards for extensive discussion over the years about salticid relationships, and for hastening his publication on freyines on which this paper relied. I thank Gustavo Ruiz for his collaborations on salticid relationships, and for his hard work on various projects that served as prerequisites for this paper. He was generous and helpful with his advice, not only correcting errors but also permitting me to use his unpublished results on the placement of several Neotropical genera. I am grateful to Tamás Szűts for sharing his unpublished photographs of type specimens. Special thanks are due to Suresh Benjamin, Charles Haddad, Shuqiang Li, Jürgen Otto, Michael Schäfer, and Vida Van der Walt for permitting me to use their photographs of living spiders. Gustavo Ruiz, Martín Ramírez, Mark Harvey, G.B. Edwards, Michael Rix, and an anonymous reviewer gave helpful comments on the manuscript. I am thankful to Robert Suter, Rick Vetter, and Michael Rix for their extraordinary efforts in guiding this paper to publication. This paper was supported by an NSERC Discovery grant.



Figures 2–7.—**Onomastinae**: 2, *Onomastus pethiyagodai* Benjamin, 2010, female, Sri Lanka (photo from Benjamin 2010, fig. 18D). **Asemoneinae**: ,3 *Asemonea* sp., female, Gabon: Lambaréné; 4, *Asemonea tenuipes* (O. Pickard-Cambridge, 1869), male, Singapore. **Lyssomaninae**: 5, *Chinoscopus* cf. *flavus* (Peckham, Peckham & Wheeler, 1889), female, Panama; 6, *Lyssomanes jemineus* Peekham, Peckham & Wheeler, 1889, male, México: Campeche; 7, *Lyssomanes temis* Peckham, Peckham & Wheeler, 1889, female, Ecuador: Yasuní. Figure 2 is © 2010 The Linnean Society of London, with permission. Figures 3–7 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.

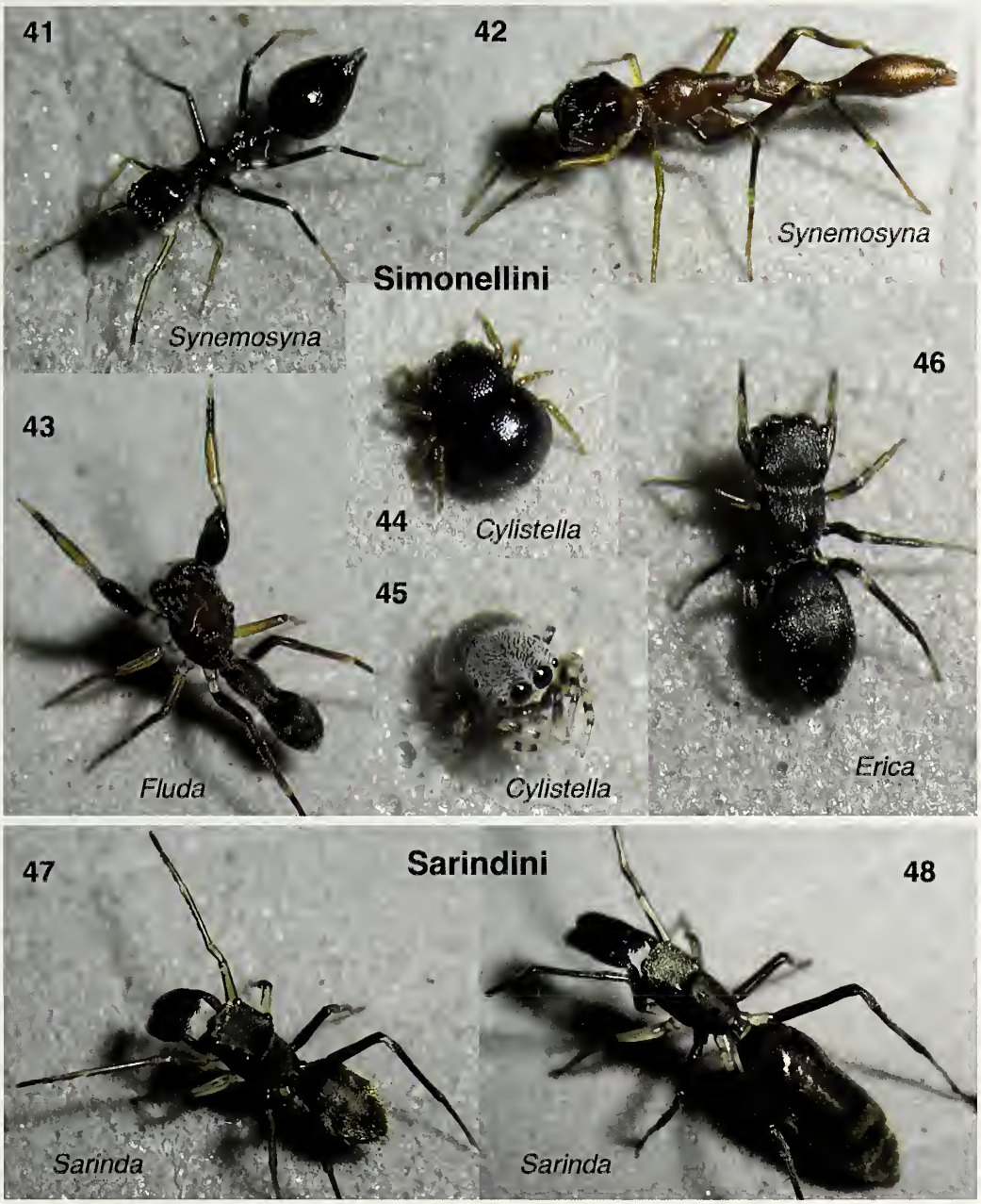
Figures 8–14.—Spartaeinae. **Spartaeini**: 8, *Gelotia bimaculata* Thorell, 1890, male, Malaysia: Sarawak: Kubah Nat. Pk.; 9, *Cocalus murinus* Simon, 1899, female, Singapore; 10, *Neobrettus* sp., female, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; 11, *Mintonia silvicola* Wanless, 1987, male, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; 12, *Cyrba* sp., male, Gabon: Estuaire, Cap Esterias; 13, *Portia* sp., female, Gabon: Ngounié: Waka Nat. Pk.; 14, *Holcolaetis vellerea* (Simon, 1910), male, South Africa: Pretoria: Kameeldrift, Pretoria (photo by Vida Van der Walt). Figures 8–13 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license. Figure 14 is © 2014 Vida Van der Walt, used with permission.

Figures 15–20.—Spartaeinae. **Lapsiini:** 15, *Galianora sacha* Maddison, 2006, male, Ecuador: Orellana: Río Bigal Reserve; 16, *Thrandina parocula* Maddison, 2006, male, Ecuador: Napo: Río Guamani; 17, *Galianora bryicola* Maddison, 2006, male, Ecuador: Orellana: Río Bigal Reserve. **Cocalodini:** 18, *Tabuina varirata* Maddison, 2009, female, Papua New Guinea: Varirata National Park; 19, *Cocalodes longicornis* Wanless, 1982, male, Papua New Guinea: Varirata National Park; 20, *Cucudeta zabkai* Maddison, 2009 — Papua New Guinea: Southern Highlands Province, Wanakipa. Figures 15, 17–20 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license. Figure 16 is © 2012 W. P. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.

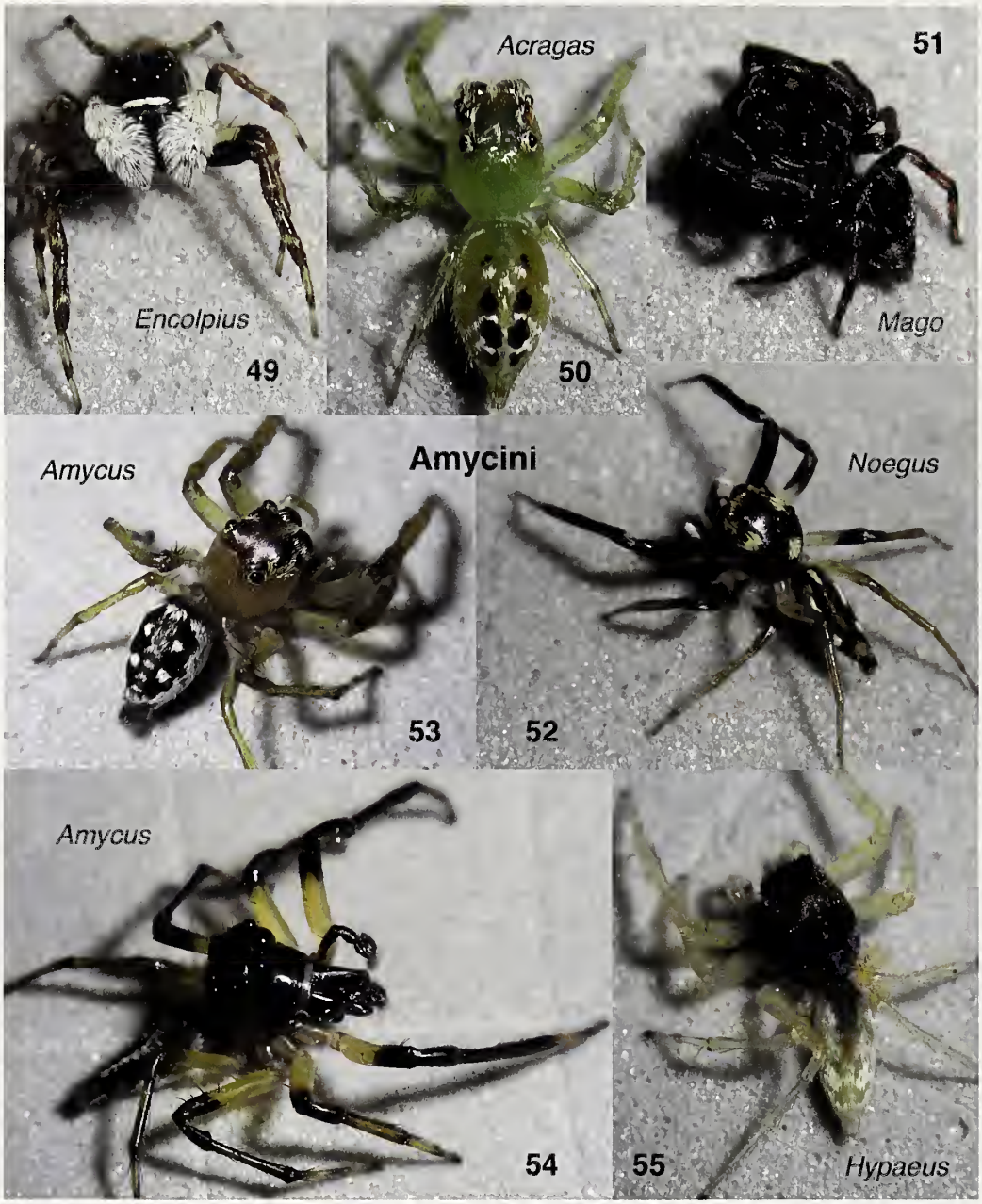
Figures 21–27.—**Eupoinae**: 21, 22, *Sinoinsula curva* (Zhou & Li, 2013), male and female in copula, China: Hainan: Mt. Limushan (photos by Yuanye Zhou). **Hisponinae**: 23, *Tomomingi* sp., female, Gabon: Monts de Cristal, Tchimbélé; 24, *Jerzego corticicola* Maddison, 2014, female, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; 25, *Jerzego* cf. *alboguttatus* (Simon, 1903), juvenile, Malaysia: Sarawak: Lambir Hills Nat.; 26, *Massagris honesta* Wesołowska, 1993, female, South Africa: Eastern Cape, Hogsback (photo by Charles Haddad); 27, *Massagris natalensis* Wesołowska & Haddad, 2009, female, South Africa: Kwazulu Natal, Ndumo (photo by Vida Van der Walt). Figure 21 is from Zhou & Li (2013a: fig. 118) and is © 2013 Magnolia Press, with permission. Figure 22 is © 2013 Yuanye Zhou & Shuqiang Li, released under a Creative Commons Attribution (CC-BY) 3.0 license. Figures 23–25 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license. Figure 26 is © 2010, Charles Haddad, used with permission. Figure 27 is © 2015 Vida Van der Walt, used with permission.

Figures 28–34.—Salticinae: Amycoida. **Gophoini:** 28, *Ceriomura* sp., female, Ecuador: Yasuní; 29, *Cotinusa* cf. *distincta* (Peckham & Peckham, 1888), male, México: Jalisco; 30, *Colonus* sp., México: Jalisco. **Bredini:** 31, *Breda akypueruna* Ruiz & Brescovit, 2013, male, Ecuador: Yasuní. **Sitticini:** 32, *Aillutticus nitens* Galiano, 1987, male, Uruguay: Canelones: Barra de Carrasco; 33, *Jollas* sp., male, Ecuador: Yasuní; 34, *Sitticus pubescens* (Fabricius 1775), female, Poland: near Neple. Figures 28–34 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.

Figures 35–40.—Salticinae: Amycoida. **Huriini:** 35, *Hurius* sp. male, Ecuador, Pichincha: near Paso de la Virgen. **Thiodinini:** 36, *Cyllodania* sp., female, Ecuador: Esmeraldas: Reserva Canandé; 37, cf. *Arachnomura* sp., male, Ecuador: Yasuní; 38, *Titanattus* sp., male, Ecuador: Pichincha: Bellavista Cloud Forest Reserve. **Scopocirini:** 39, *Gypogyna* sp., male, México: Jalisco; 40, *Scopocira* cf. *cepa* Costa & Ruiz, 2014, male, Ecuador: Yasuní. Figures 35–39 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 lieense. Figure 40 is © 2014 W. Maddison, released under a Creative Commons Attribution 4.0 International license.



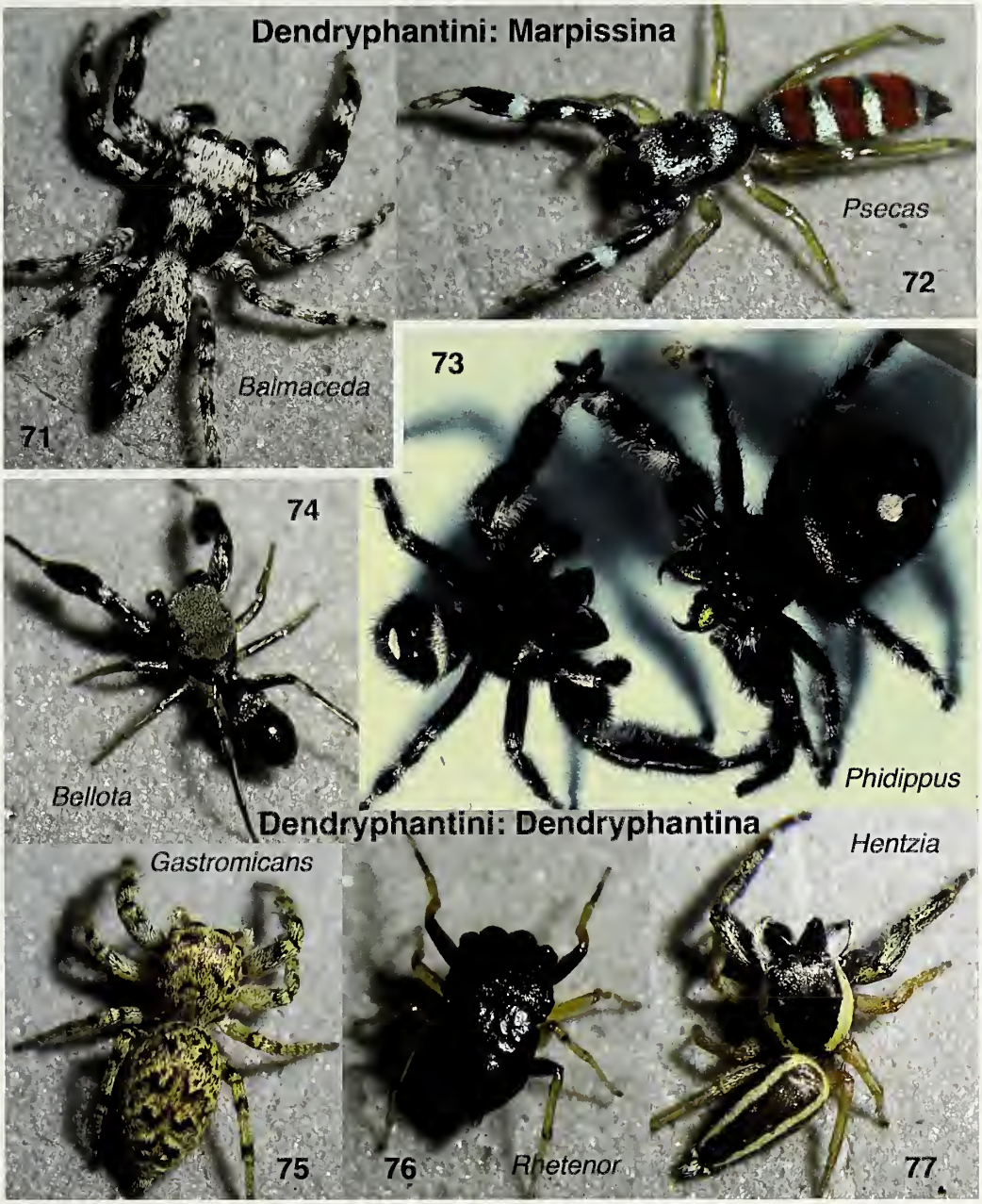
Figures 41–48.—Salticinae: Amycoida. **Simonellini:** 41, *Synemosyna* sp., female, Ecuador: Esmeraldas: Reserva Canandé; 42, *Synemosyna* sp. female, Ecuador: Yasuní; 43, *Fluda* sp., male, Ecuador: Orellana: Río Bigal Reserve; 44, *Cylistella* sp., female, México: Jalisco, Chamela; 45, *Cylistella* sp., female, Ecuador: Yasuní; 46, *Erica* sp., female, Ecuador: Yasuní. **Sarindini:** 47, *Sarinda* sp., female, Ecuador: Yasuní; 48, *Sarinda* cf. *nigra* Peckham & Peckham, 1892, female, Ecuador: Yasuní. Figures 41–48 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.



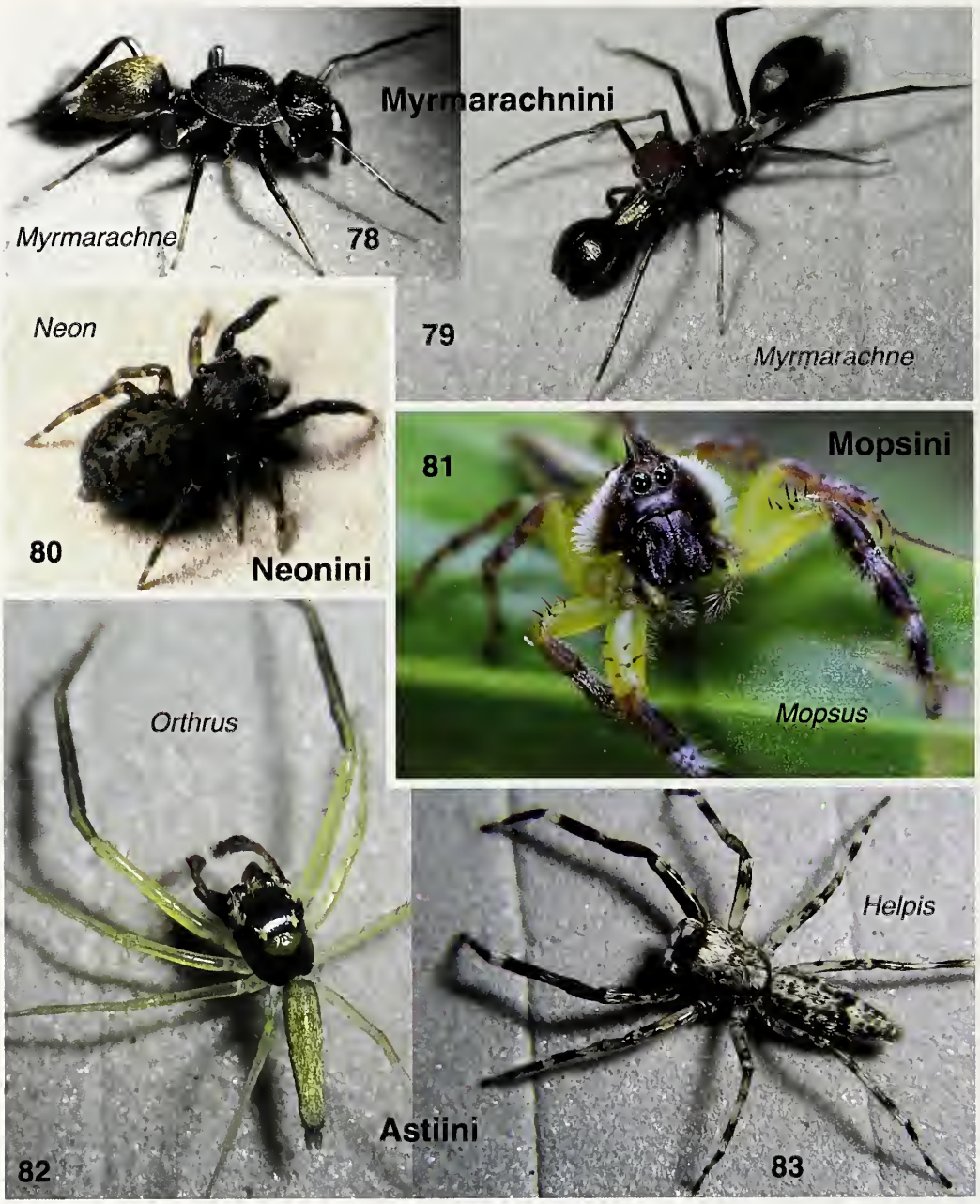
Figures 49–55.—Salticinae: Amycoida. **Amycini:** 49, *Encolpius* sp., male, Ecuador: Napo: Río Guamani; 50, *Acragas longimanus* Simon, 1900, female, Ecuador: Yasuní; 51, *Mago* sp., male, Ecuador: Esmeraldas: Reserva Canandé; 52, *Noegus* cf. *actinosus* Simon, 1900, male, Ecuador: Yasuní; 53, *Amycus* sp., female, Ecuador: Yasuní; 54, *Amycus* sp., male, Ecuador: Yasuní; 55, *Hypaeus* aff. *porcatus* (Taczanowski, 1871), male, Ecuador: Yasuní. Figures 49–55 are

Figures 56–63.—Salticinae: Salticoida. **Agoriini:** 56, *Agorius* sp., male, Malaysia: Sarawak: Kubah Nat. Pk.; 57, *Agorius* sp., male, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; **Baviini:** 58, unidentified baviine, male, Malaysia: Sarawak: Lambir Hills Nat. Pk.; 59, *Bavia* sp., female, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; **Marpissoida: Ballini:** 60, *Pachyballus* sp., female, Gabon: Monts de Cristal, Tchimbélé; 61, *Leikung porosa* (Wanless, 1978), male, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; 62, *Mantisatta longicauda* Cutler & Wanless, 1973, female, Philippines: Laguna Province: Los Baños; 63, *Ballus chalybeius* (Walckenaer, 1802), female, Poland: Janów Podiaski.

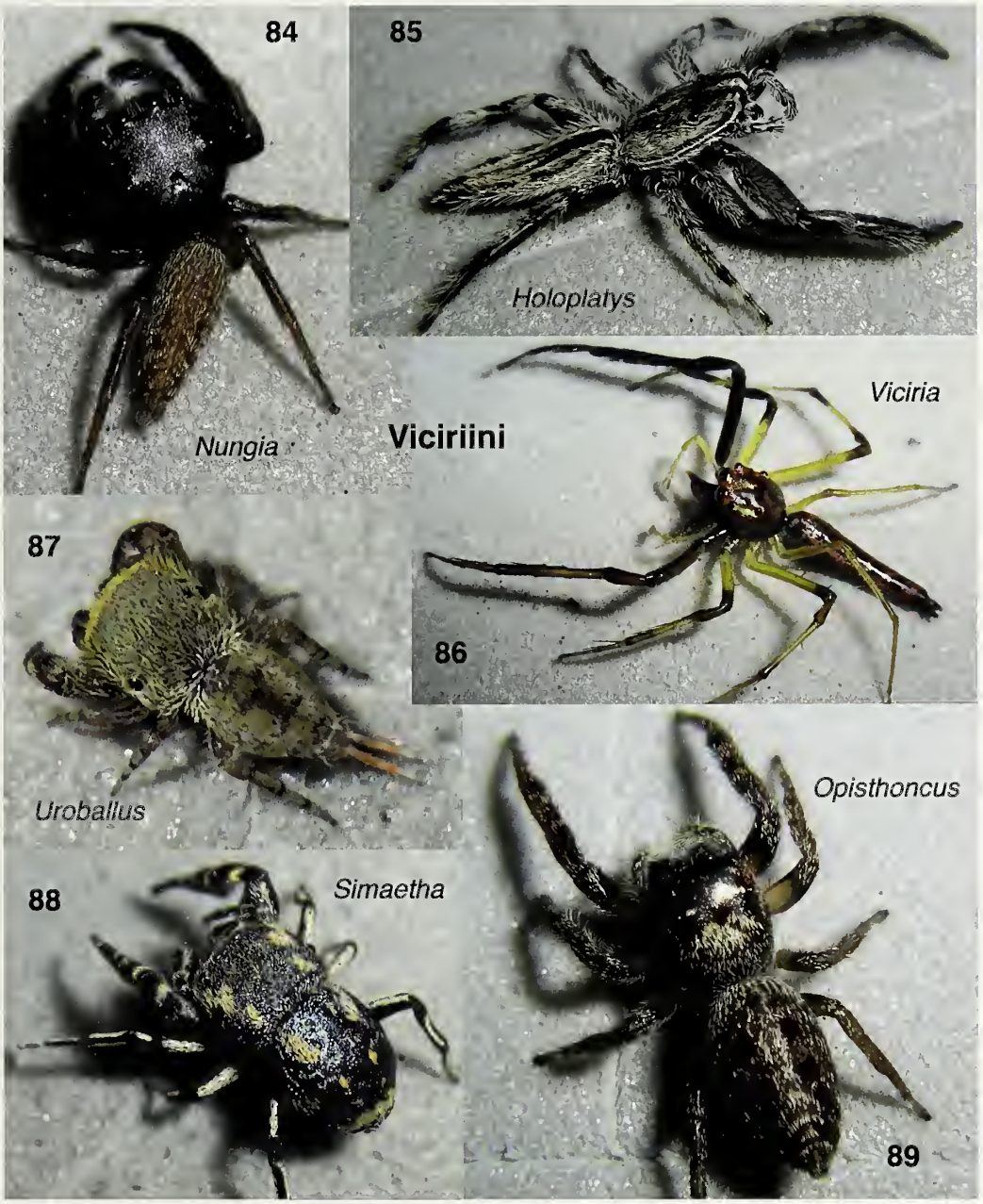
Figures 64–70.—Salticinae: Salticoida: Marpissoida. **Tisanibini:** 64, *Tisaniba uulu* Zhang & Maddison, 2014, female, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; 65, *Tisaniba uulu* Zhang & Maddison, 2014, male, Malaysia: Sarawak: Gunung Mulu Nat. Pk. **Dendryphantini: Itatina:** 66, *Itata* sp., male, Ecuador: Yasuní. **Dendryphantini: Synagelina:** 67, *Attidops youngii* (Peckham & Peckham, 1888), male, Canada: Ontario: Port Cunnington; 68, *Peckhamia* sp., female, México: Jalisco; 69, *Synageles* sp., female, U.S.A.: Arizona: Santa Rita Mountains; 70, *Admestina* sp., female, U.S.A.: Florida: Gainesville. Figures 64–70 are



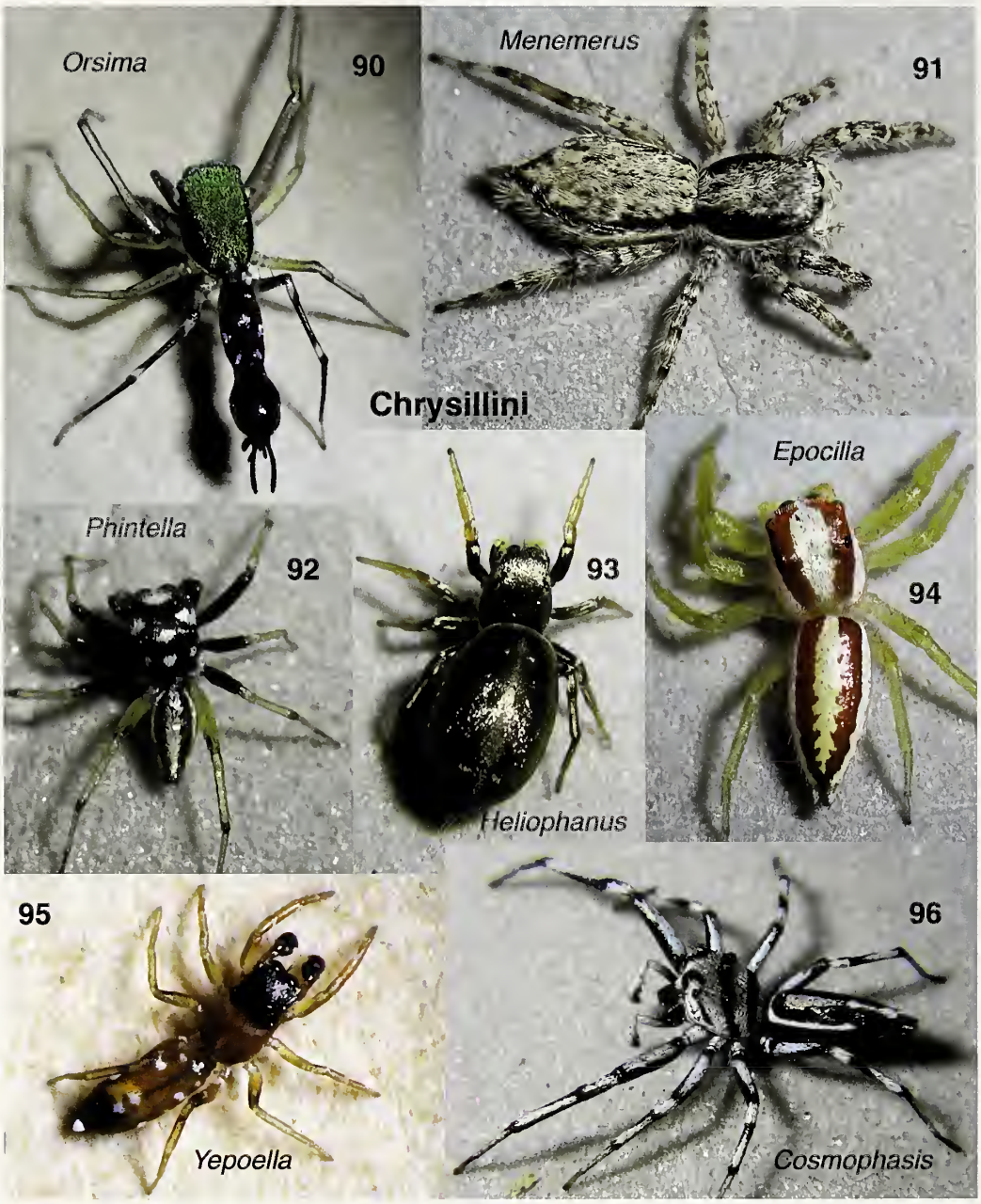
Figures 71–77.—Salticinae: Salticoida: Marpissoida: Dendryphantini. **Marpissina:** 71, *Balmaceda* sp., male, Ecuador: Yasuní; 72, *Psecas* sp., female, Ecuador: Yasuní. **Dendryphantina:** 73, *Phidippus audax* (Hentz, 1845), male and female, Canada: Ontario: Burlington; 74, *Bellota* sp., male, Ecuador: Esmeraldas: Reserva Canandé; 75, *Gastromicans* sp., female, Ecuador: Yasuní; 76, *Rhetenor* sp., female, Ecuador: Yasuní; 77, *Hentzia* sp., male, Dominican Republic: Barahona: Parque Nacional Sierra Martín García. Figures 71–77 are



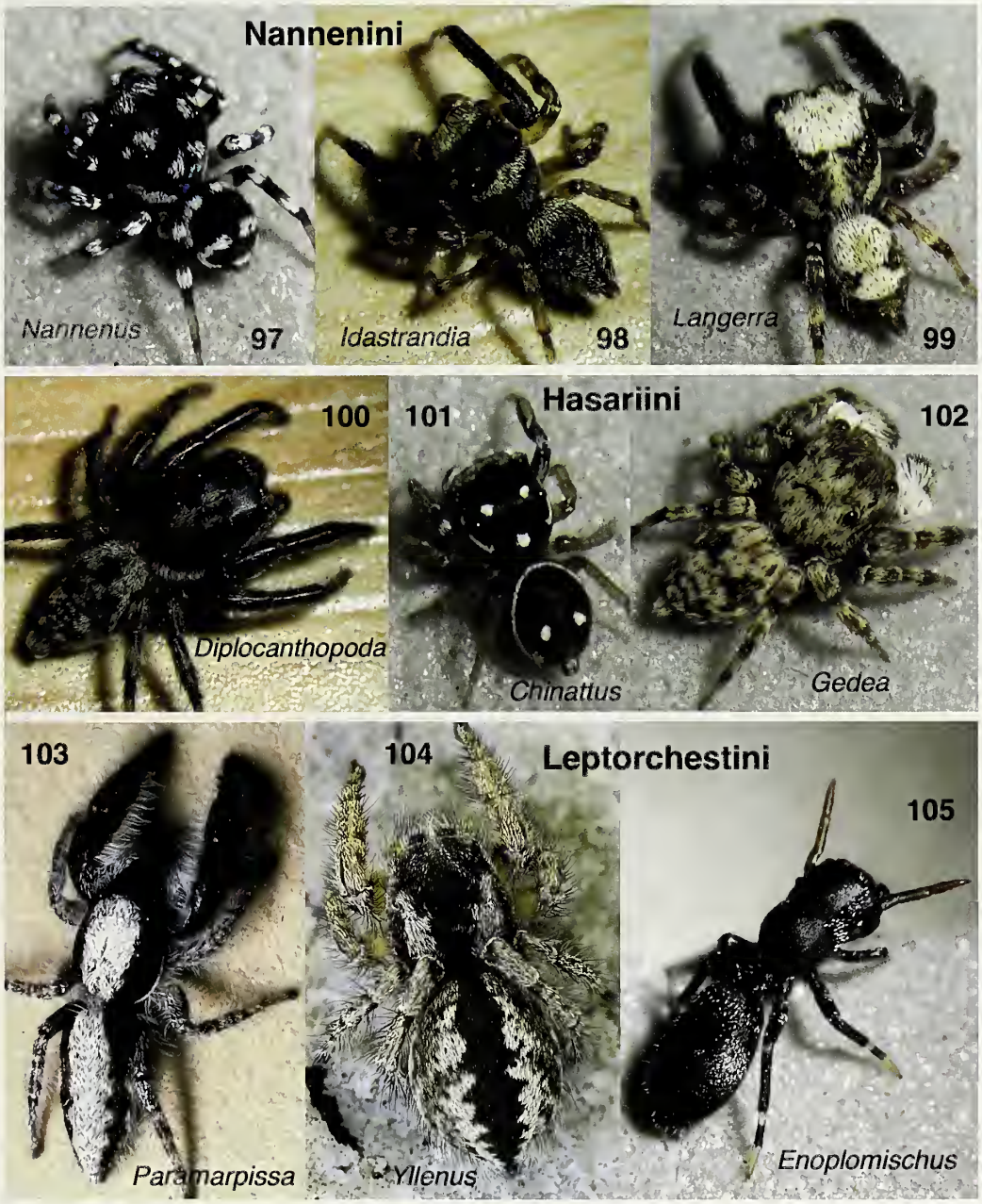
Figures 78–83.—Salticinae: Salticoida: Astioida. **Myrmarachnini:** 78, *Myrmarachne* sp., female, Gabon: Ngounié: Waka Nat. Park; 79, *Myrmarachne alticephalon* Yamasaki & Ahmad, 2013, male, Malaysia: Sarawak: Gunung Mulu Nat. Pk. **Neonini:** 80, *Neon* sp., female, U.S.A.: California: Monterey County. **Mopsini:** 81, *Mopsus mormon* Karsch, 1878, male, Australia: Queensland: Townsville (photo by Jürgen Otto). **Astiini:** 82, *Orthrus* cf. *muluensis* Wanless, 1980, male, Malaysia: Sarawak: Lambir Hills Nat. Pk.; 83, *Helpis minitabunda* (L. Koch, 1880), male, Papua New Guinea: Enga Province: Porgera. Figure 81 is © 2004 Jürgen Otto, used with permission. Figures 78–80, 82, 83 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.



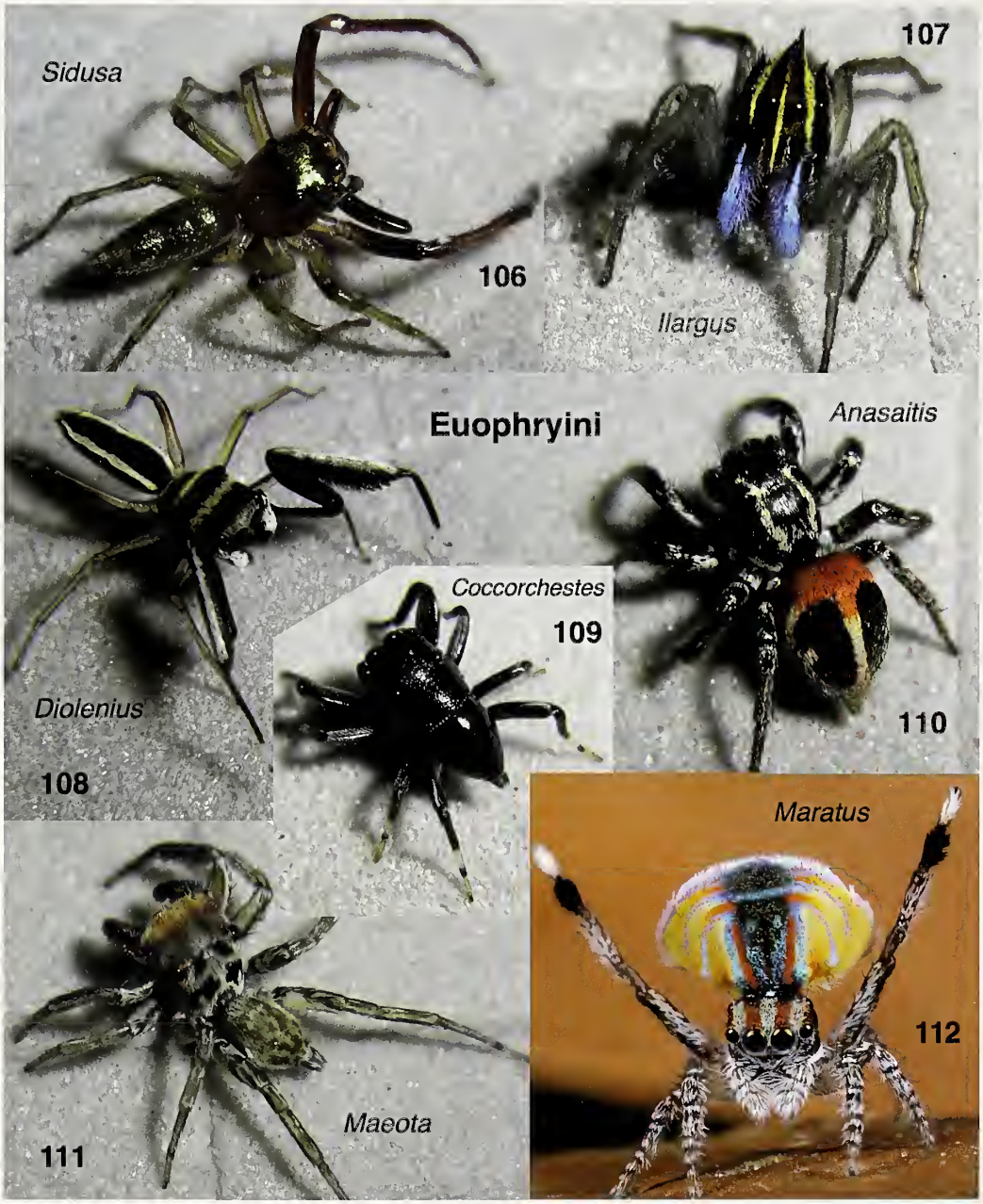
Figures 84–89.—Salticinae: Salticoida: Astioida. **Viciriini:** 84, *Nungia* sp., male, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; 85, *Holoplatys* sp., male, Papua New Guinea: Southern Highlands Province: Wanakipa; 86, *Viciria praemandibularis* (Hasselt, 1893), male, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; 87, *Uroballus* sp., male, Malaysia: Sarawak: Lambir Hills Nat. Pk.; 88, *Simaetha* sp., female, Malaysia: Sarawak: Lambir Hills Nat. Pk.; 89, *Opisthoncus* sp., female, Papua New Guinea: Enga Province: Kai-ingri.



Figures 90–96.—Salticinae: Salticoida: Saltafresia. **Chrysillini:** 90, *Orsima ichneumon* (Simon, 1901), male, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; 91, *Menemerus bivittatus* (Dufour, 1831), female, Ecuador: Yasuní; 92, *Phintella* sp., male, Malaysia: Sarawak: Kubah Nat. Pk.; 93, *Heliophanus* sp., female, Poland: near Stary Bubel; 94, *Epocilla* sp., female, Malaysia: Sarawak: Bako Nat. Pk.; 95, *Yepoella* sp., male, Ecuador: Sucumbios: Reserva Faunistica Cuyabeno; 96, *Cosmophasis* sp., male, Papua New Guinea: Southern Highlands Province: Wanakipa. Figures 90–96 are



Figures 97–105.—Salticinae: Salticoida: Saltafresia. **Nannenini:** 97, *Nannenus syrphus* Simon, 1902, male, Malaysia: Sarawak: Lambir Hills Nat. Pk.; 98, *Idastrandia* cf. *orientalis* (Szombathy, 1915), male, Singapore; 99, *Langerra* aff. *longicymbium* Song & Chai, 1991, male, Malaysia: Sarawak: Lambir Hills Nat. Pk. **Hasariini:** 100, *Diplocanthopoda marina* Abraham, 1925, male, Singapore; 101, *Chinattus* sp., male, Malaysia: Sarawak: Lambir Hills Nat. Pk.; 102, *Gedea* sp., male, Malaysia: Sarawak: Gunung Mulu Nat. Pk. **Leptorchestini:** 103, *Paramarpissa* sp., male, U.S.A.: California: San Luis Obispo County; 104, *Yllenus vittatus* Thorell, 1875, female, Austria (photo by Michael Schäfer, from http://www.kleinesganzgross.de/gallery_art.php?ID=85); 105, *Enoplomischus* sp, juvenile, Gabon: Ngounié: Waka Nat. Park. Figures 97–103,105 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license. Figure 104 is © 2014 Michael Schäfer, used with permission.

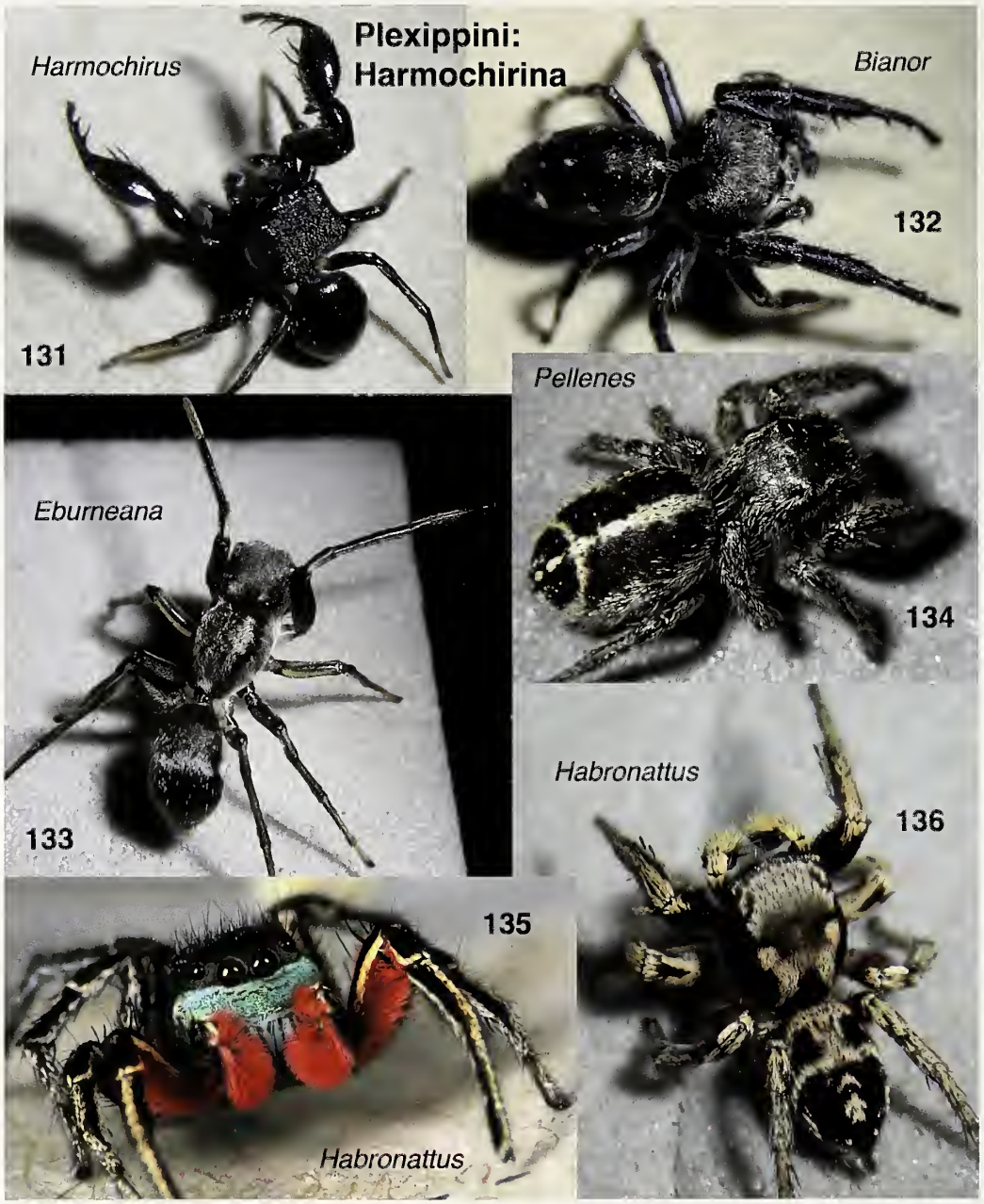


Figures 106–112.—Salticinae: Salticoida: Saltafresia. **Euophryini:** 106, *Sidusa* sp., male, Ecuador: Esmeraldas: Puerto Nuevo; 107, *Ilargus* sp., male, Ecuador: Pichincha: near Nono; 108, *Diolenius* sp., male, Papua New Guinea: Central Province: Varirata National Park; 109, *Coccorchestes* sp., male, Papua New Guinea: Southern Highlands Province: Wanakipa; 110, *Anasaitis elegantissima* (Simon, 1888), female, Dominican Republic: La Altagracia: Punta Cana; 111, *Maeota* sp., male, Ecuador: Tena; 112, *Maratus volans* (O. Pickard-Cambridge, 1874), male (photo by Jürgen Otto). Figures 106–110 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license. Figure 111 is © 2015 W. P. Maddison & J. Zhang, released under a Creative Commons Attribution (CC-BY) 3.0 license. Figure 112 is © 2010 Jürgen Otto, used with permission.

Figures 113–118.—Salticinae: Salticoida: Saltafresia. **Salticini:** 113, *Tusitala* sp., male, Gabon: Moyen-Ogooué: Lambaréné; 114, *Carrhotus sannio* (Thorell, 1877), male, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; 115, *Salticus* sp., female, U.S.A.: Arizona: near Santa Rita Mountains. **Aelurillini: Aelurillina:** 116, *Langelurillus* sp., female, Gabon: Monts de Cristal, Tchimbélé; 117, *Stenaelurillus* sp., male, Gabon: Estuaire: Cap Esterias; 118, *Phlegra* sp., female, Germany: Saxony: Authausen.

Figures 119–124.—Salticinae: Salticoida: Saltafresia: Aelurillini. **Freyina:** 119, *Freya decorata* (C.L. Koch, 1846), male, Ecuador: Yasuní; 120, *Asaracus* sp., male, Ecuador: Yasuní; 121, *Akela* sp., male, Ecuador: Napo: Río Salado at highway 45. **Thiratoscirtina:** 122, *Longarenus* sp., female, Gabon: Monts de Cristal, Tchimbélé; 123, *Thiratoscirtus* sp., male, Gabon: Monts de Cristal, Tchimbélé; 124, *Malloneta guineensis* Simon, 1902, male, Gabon: Ngounié: Waka Nat. Park. Figures 119–124 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.

Figures 125–130.—Salticinae: Salticoida: Saltafresia: Plexippini. **Plexippina:** 125, *Plexippus paykulli* (Audouin, 1826), male, Singapore; 126, *Hermotimus* sp., female, Gabon: Ngounié: Waka Nat. Park; 127, *Evarcha falcata* (Clerck, 1757), male, Spain: Barcelona: Bagà; 128, *Hyllus* cf. *keratodes* (Hasselt, 1882), male, Malaysia: Selangor: near Ulu Gombak; 129, *Telamonia dimidiata* (Simon, 1899), female, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; 130, *Epeus* sp., male, Malaysia: Pahang: Cameron Highlands. Figures 125–130 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.



Figures 131–136.—Salticinae: Salticoida: Saltafresia: Plexippini. **Harmochirina:** 131, *Harmochirus* sp., male, Malaysia: Selangor: Ulu Gombak Field Station; 132, *Bianor* sp., male, Malaysia: Pahang: Cameron Highlands; 133, *Eburneana* sp., male, Gabon: Monts de Cristal, Tchimbélé; 134, *Pellenes tripunctatus* (Walckenaer, 1802), female, Germany: Saxony: Authausen; 135, *Habronattus americanus* (Keyserling, 1885), male, U.S.A.: Idaho; 136, *Habronattus mexicanus* (Peckham & Peckham, 1896), male, México: Jalisco. Figures 131–136 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.

Table 2.—Classification of genera of Salticidae. ? = placement especially tentative; * = placement in part by molecular data (Hedin & Maddison 2001; Maddison & Hedin 2003a, b; Su et al. 2007; Andriamalala 2007; Maddison et al. 2008, 2014; Bodner & Maddison 2012; Zhang & Maddison 2013, 2014; Ruiz & Maddison in press; Maddison, unpublished data). Available in machine-readable form online at http://dx.doi.org/10.1636/R15-55.s1, http://doi.org/10.5886/gg3ud66w, and http://salticidae.org/classification/. This table is © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.

Subfamily Onomastinae

(12 species in 1 genus)

Onomastus Simon, 1900*

Subfamily Asemoneinae

(38 species in 5 genera)

Asemonea O. P.-Cambridge, 1869*
Goleba Wanless, 1980*
Hindumanes Logunov, 2004
Macopaeus Simon, 1900
Pandisus Simon, 1900*

Subfamily Lyssomaninae

(92 species in 2 genera)

Chinoscopus Simon, 1900*
Lyssomanes Hentz, 1845*

Subfamily Spartaeinae

(165 species in 29 genera)

Tribe Spartaeini: Subtribe Spartaeina (111 species in 16 genera)

Brettus Thorell, 1895*
Cocalus C. L. Koch, 1846*
Cyrba Simon, 1876*
Gelotia Thorell, 1890*
Meleon Wanless, 1984*
Mintonia Wanless, 1984*
Neobrettus Wanless, 1984*
Paracyrba Żabka & Kovac, 1996*
Phaeacius Simon, 1900*
Portia Karsch, 1878*
Sparbambus Zhang, Woon & Li, 2006*
Spartaeus Thorell, 1891*
Taraxella Wanless, 1984*
Veissella Wanless, 1984
Wanlessia Wijesinghe, 1992
Yaginumanis Wanless, 1984

Tribe Spartaeini: Subtribe Holcolaetina (9 species in 2 genera)

Holcolaetis Simon, 1886*
Sonoita Peckham & Peckham, 1903*

Tribe Cocalodini (25 species in 6 genera)

Allococalodes Wanless, 1982*
Cocalodes Pocock, 1897*
Cucudeta Maddison, 2009*
Depreissia Lessert, 1942*
Tabuina Maddison, 2009*
Yamangalea Maddison, 2009*

Tribe Lapsiini (20 species in 5 genera)

Galianora Maddison, 2006*
Lapsamita Ruiz, 2013
Lapsias Simon, 1900*
Soesiladeepakius Makhan, 2007*
Thrandina Maddison, 2006*

Subfamily Eupoinae

(34 species in 3 genera)

Eupoa Żabka, 1985*
Corusca Zhou & Li, 2013
Sinoinsula Zhou & Li, 2013

Subfamily Hisponinae

(53 species in 9 genera)

†*Almolinus* Petrunkevitch, 1958
†*Gorgopsina* Petrunkevitch, 1955
Hispo Simon, 1886*
Jerzego Maddison, 2014*
Massagris Simon, 1900*
†*Prolinus* Petrunkevitch, 1958
Tomobella Szűts & Scharff, 2009*
Tomocyrba Simon, 1900*
Tomomingi Szűts & Scharff, 2009*

Subfamily Salticinae

(5379 species in 538 genera)

Salticinae: Clade Amycoida

(430 species in 63 genera)

Tribe Gophoini (59 species in 8 genera)
Banksetosa Chickering, 1946
Carabella Chickering, 1946*
Ceriomura Simon, 1901*
Colonus F. O. P.-Cambridge, 1901*
Cotinusa Simon, 1900*
Nilakantha Peckham & Peckham, 1901*
Parathiodina Bryant, 1943
Proctonemesia Bauab & Soares, 1978

Tribe Sitticini (120 species in 10 genera)
Aillutticus Galiano, 1987*
Amatorculus Ruiz & Brescovit, 2005
Attulus Simon, 1889*
Capeta Ruiz & Brescovit, 2005
Gavarilla Ruiz & Brescovit, 2006
Jollas Simon, 1901*
Nosferattus Ruiz & Brescovit, 2005
Pseudattulus Caporiacco, 1947
Semiopyla Simon, 1901
Sitticus Simon, 1901*

Tribe Bredini (14 species in 2 genera)
Breda Peckham & Peckham, 1894*
Druzia Ruiz & Brescovit, 2013

Tribe Scopocirini (10 species in 2 genera)
Gypogyna Simon, 1900*
Scopocira Simon, 1900*

Tribe Thiodinini (24 species in 9 genera)
Agelista Simon, 1900*
Arachnomura Mello-Leitão, 1917*
Atomosphyrus Simon, 1902
Bredana Gertsch, 1936
Cyllodania Simon, 1902*
Hyetussa Simon, 1902*
Micalula Strand, 1932
Thiodina Simon, 1900
Titanattus Peckham & Peckham, 1885*

Tribe Sarindini (36 species in 7 genera)
Corcovetella Galiano, 1975
Martella Peckham & Peckham, 1892*
Parafluda Chickering, 1946
Sarinda Peckham & Peckham, 1892*
Simprulla Simon, 1901
Tanybelus Simon, 1902
Zuniga Peckham & Peckham, 1892*

Tribe Simonellini (39 species in 4 genera)
Cylistella Simon, 1901*
Erica Peckham & Peckham, 1892*
Fluda Peckham & Peckham, 1892*
Synemosyna Hentz, 1846*

Tribe Huriini (16 species in 6 genera)
Admesturius Galiano, 1988
Atelurius Simon, 1901
Hurius Simon, 1901*
Scoturius Simon, 1901
Simonurius Galiano, 1988
Urupuyu Ruiz & Maddison, 2015*

Tribe Amycini (110 species in 13 genera)
Acragas Simon, 1900*
Amycus C. L. Koch, 1846*
Anaurus Simon, 1900
Arnoliseus Braul, 2002
Encolpius Simon, 1900*
Frespera Braul & Lise, 2002*
Hypaeus Simon, 1900*
Letoia Simon, 1900*
Macutula Ruiz, 2011
Maenola Simon, 1900
Mago O. P.-Cambridge, 1882*
Noegus Simon, 1900*
Vinnius Simon, 1902

Amycoida *incertae sedis* (2 species in 2 genera)
Orvilleus Chickering, 1946
Toloella Chickering, 1946

Salticinae: Clade Salticoida

(4825 species in 427 genera)

Tribe Agoriini (45 species in 2 genera)
Agorius Thorell, 1877*
Synagelides Strand, 1906*

Tribe Baviini (26 species in 3 genera)
Bavia Simon, 1877*
Piranthus Thorell, 1895?
Stagetillus Simon, 1885

Salticoida: Astioida

(584 species in 55 genera)

Tribe Myrmarachnini (246 species in 7 genera)

Belippo Simon, 1910*
Bocus Peckham & Peckham, 1892
Damoetas Peckham & Peekham, 1886
Judalana Rix, 1999
Ligonipes Karsch, 1878*
Myrmarachne MacLeay, 1839*
Rhombonotus L. Koch, 1879

Tribe Neonini (27 species in 1 genus)

Neon Simon, 1876*

Tribe Astiini (54 species in 11 genera)

Arasia Simon, 1901*
Astia L. Koch, 1879
Astilodes Żabka, 2009?
Helpis Simon, 1901*
Jacksonoides Wanless, 1988*
Katya Prószyński & Deeleman-Reinhold, 2010?
Megaloastia Żabka, 1995
Orthrus Simon, 1900*
Parahelpis Gardzińska & Żabka, 2010
Sondra Wanless, 1988*
Tauala Wanless, 1988*

Tribe Mopsini (12 species in 3 genera)

Mopsolodes Żabka, 1991
Mopsus Karsch, 1878*
Sandalodes Keyserling, 1883*

Tribe Viciriini (other than Simaethina) (176 species in, 20 genera)

Abracadabrella Żabka, 1991?
Avarua Marples, 1955
Clynotis Simon, 1901*
Corambis Simon, 1901*
Holoplatys Simon, 1885*
Huntiglennia Żabka & Gray, 2004
Lystrocteisa Simon, 1884?
Nungia Żabka, 1985*
Ocrisiona Simon, 1901*
Opisthoncus L. Koch, 1880*
Paraphilaeus Żabka, 2003?
Paraplatoides Żabka, 1992
Penionomus Simon, 1903*
Pungalina Richardson, 2013?
Rhondes Simon, 1901*
Rogmocrypta Simon, 1900?
Tara Peckham & Peckham, 1886
Trite Simon, 1885*
Viciria Thorell, 1877*
Zebraplatys Żabka, 1992

Tribe Viciriini: Subtribe Simaethina (69 species in 13 genera)

Heratemita Strand, 1932*
Iona Peckham & Peckham, 1886
Irura Peckham & Peckham, 1901*
Ligurra Simon, 1903*
Mantius Thorell, 1891
Phyaces Simon, 1902
Poecilorchestes Simon, 1901
Porius Thorell, 1892
Simaetha Thorell, 1881*
Simaethula Simon, 1902
Stertinius Simon, 1890?
Uroballus Simon, 1902*
Urogelides Żabka, 2009

Salticoida: Marpissoida

(840 species in 90 genera)

Tribe Ballini (85 species in 15 genera)

Afromarengo Benjamin, 2004*
Ballus C. L. Koch, 1850*
Colaxes Simon, 1900
Copocrossa Simon, 1901
Cynapes Simon, 1900
Goleta Peckham & Peckham, 1894
Indomarengo Benjamin, 2004
Leikung Benjamin, 2004*
Mantisatta Warburton, 1900*
Marengo Peckham & Peckham, 1892*
Pachyballus Simon, 1900*
Padilla Peckham & Peckham, 1894*
Peplometus Simon, 1900*
Philates Simon, 1900
Sadies Wanless, 1984

Tribe Tisanibini (6 species in 2 genera)

Saaristattus Logunov & Azarkina, 2008?
Tisaniba Zhang & Maddison, 2014*

Tribe Dendryphantini: Subtribe Synagelina (48 speeies in 6 genera)

Admestina Peckham & Peckham, 1888*
Attidops Banks, 1905*
Cheliferoides F. O. P.-Cambridge, 1901*
Descanso Peckham & Peckham, 1892
Peckhamia Simon, 1901*
Synageles Simon, 1876*

Tribe Dendryphantini: Subtribe Itatina (5 species in 1 genus)

Itata Peckham & Peckham, 1894*

Tribe Dendryphantini: Subtribe Marpissina (110 species in 9 genera)

Balmaceda Peckham & Peckham, 1894*
Empanda Simon, 1903
Fuentes Peckham & Peckham, 1894
Maevia C. L. Koch, 1846*
Marpissa C. L. Koch, 1846*
Mendoza Peckham & Peekham, 1894
Metacyrba F. O. P.-Cambridge, 1901*
Platycryptus Hill, 1979*
Psecas C. L. Koch, 1850*

Tribe Dendryphantini: Subtribe Dendryphantina (581 species in 56 genera)

Alcmena C. L. Koch, 1846
Anokopsis Bauab & Soares, 1980
Anicius Chamberlin, 1925
Ashtabula Peckham & Peckham, 1894*
Avitus Peckham & Peckham, 1896
Bagheera Peckham & Peckham, 1896
Beata Peckham & Peckham, 1895*
Bellota Peckham & Peckham, 1892*
Bryantella Chickering, 1946*
Cerionesta Simon, 1901
Chirothecia Taczanowski, 1878*
Dendryphantes C. L. Koch, 1837*
Donaldius Chickering, 1946
Eris C. L. Koch, 1846*
Fritzia O. P.-Cambridge, 1879*
Gastromicans Mello-Leitão, 1917*
Ghelna Maddison, 1996*
Hentzia Marx, 1883*
Lurio Simon, 1901
Mabellina Chickering, 1946*
Macaroeris Wunderlich, 1992
Mburuvicha Scioscia, 1993
Messua Peckham & Peckham, 1896*
Metaphidippus F. O. P.-Cambridge, 1901
Mirandia Badcock, 1932[?]
Monaga Chickering, 1946
Nagaina Peckham & Peckham, 1896
Naubolus Simon, 1901
Osericta Simon, 1901
Paradamoetas Peckham & Peckham, 1885
Paraphidippus F. O. P.-Cambridge, 1901*
Parnaenus Peckham & Peckham, 1896
Pelegrina Franganillo, 1930*
Phanias F. O. P.-Cambridge, 1901*
Phidippus C. L. Koch, 1846*
Planiemen Wesołowska & van Harten, 2007[?]
Poultonella Peckham & Peckham, 1909*
Pseudofluda Mello-Leitão, 1928
Pseudopartona Caporiacco, 1954
Rhene Thorell, 1869*
Rhetenor Simon, 1902*
Rudra Peckham & Peckham, 1885*
Sassacus Peckham & Peckham, 1895*
Sebastira Simon, 1901
Selimus Peckham & Peckham, 1901
Semora Peckham & Peckham, 1892
Tacuna Peckham & Peckham, 1901
Terralonus Maddison, 1996*
Thammaca Simon, 1902
Tulpius Peckham & Peckham, 1896
Tutelina Simon, 1901*
Tuvaphantes Logunov, 1993
Uluella Chickering, 1946
Xuriella Wesołowska & Russell-Smith, 2000[?]
Zeuxippus Thorell, 1891
Zygoballus Peckham & Peckham, 1885[1]

Dendryphantini *incertae sedis* (5 species in 1 genus)
Semorina Simon, 1901

Salticoida: Saltafresia
(3330 species in 277 genera)

Tribe Nannenini (8 species in 3 genera)
Idastrandia Strand, 1929*
Langerra Żabka, 1985*[?]
Nannenus Simon, 1902*

Tribe Hasariini (116 speeies in 15 genera)
Bristowia Reimoser, 1934*
Cheliceroides Żabka, 1985*
Chinattus Logunov, 1999*
Curubis Simon, 1902
Diplocanthopoda Abraham, 1925*
Echeclus Thorell, 1890*
Gedea Simon, 1902*
Habrocestoides Prószyński, 1992
Habrocestum Simon, 1876*
Hasarina Schenkel, 1963
Hasarius Simon, 1871*
Imperceptus Prószyński, 1992[?]
Madhyattus Prószyński, 1992[?]
Mikrus Wesołowska, 2001
Uxuma Simon, 1902[?]

Tribe Chrysillini (599 species in 31 genera)
Afraflacilla Berland & Millot, 1941
Augustaea Szombathy, 1915
Chrysilla Thorell, 1887
Cosmophasis Simon, 1901*
Echinussa Simon, 1901
Epocilla Thorell, 1887*
Festucula Simon, 1901
Hakka Berry & Prószyński, 2001
Helicius Żabka, 1981
Heliophanillus Prószyński, 1989
Heliophanus C. L. Koch, 1833*
Helvetia Peckham & Peckham, 1894*
Icius Simon, 1876*
Jaluiticola Roewer, 1944
Kupiuka Ruiz, 2010
Marchena Peckham & Peckham, 1909*
Matagaia Ruiz, Brescovit & Freitas, 2007
Menemerus Simon, 1868*
Mexcala Peckham & Peckham, 1902*
Natta Karsch, 1879
Ogdenia Peckham & Peckham, 1908
Orsima Simon, 1901*
Paraheliophanus Clark & Benoit, 1977
Phintella Strand, 1906*
Plesiopiuka Ruiz, 2010
Pseudicius Simon, 1885*
Siler Simon, 1889*
Tasa Wesołowska, 1981
Theriella Braul & Lise, 1996
Wesolowskana Koçak & Kemal, 2008
Yepoella Galiano, 1970*

Salticoida: Saltafresia: Simonida
(2607 species in 228 genera)

Tribe Leptorchestini (92 species in 7 genera)
Araegeus Simon, 1901
Enoplomischus Giltay, 1931*
Kima Peckham & Peckham, 1902
Leptorchestes Thorell, 1870*
Paramarpissa F. O. P.-Cambridge, 1901*
Ugandinella Wesołowska, 2006
Yllenus Simon, 1868*

Tribe Euophryini (1087 species in 116 genera)

Agobardus Keyserling, 1885*
Allodecta Bryant, 1950
Amphidraus Simon, 1900*
Anasaitis Bryant, 1950*
Antillattus Bryant, 1943*
Araneotanna Özdikmen & Kury, 2006
Aruattus Logunov & Azarkina, 2008
Ascyltus Karsch, 1878
Athamas O. P.-Cambridge, 1877*
Barraina Richardson, 2013
Bathippus Thorell, 1892*
Baviola Simon, 1898?
Belliena Simon, 1902*
Bindax Thorell, 1892
Bulolia Żabka, 1996*
Bythocrotus Simon, 1903*
Canama Simon, 1903*
Caribattus Bryant, 1950
Chalcolecta Simon, 1884*
Chalcolemia Zhang & Maddison, 2012*
Chalcoscirtus Bertkau, 1880*
Chalcotropis Simon, 1902*
Chapoda Peckham & Peckham, 1896*
Charippus Thorell, 1895
Chinophrys Zhang & Maddison, 2012*
Coccorchestes Thorell, 1881*
Colyttus Thorell, 1891*
Commoris Simon, 1902
Compsodecta Simon, 1903*
Corticattus Zhang & Maddison, 2012*
Coryphasia Simon, 1902*
Corythalia C. L. Koch, 1850*
Cytaea Keyserling, 1882*
Darwinneon Cutler, 1971
Diolenius Thorell, 1870*
Ecuadattus Zhang & Maddison, 2012*
Efate Berland, 1938*
Emathis Simon, 1899*
Ergane L. Koch, 1881
Euophrys C. L. Koch, 1834*
Euryattus Thorell, 1881*
Featheroides Peng, Ying & Kim, 1994
Foliabitus Zhang & Maddison, 2012*
Frewena Richardson, 2013
Furculattus Balogh, 1980
Gorgasella Chickering, 1946?
Hypoblemum Peckham & Peckham, 1886*
Ilargus Simon, 1901*
Jotus L. Koch, 1881*
Lagnus L. Koch, 1879*
Lakarobius Berry, Beatty & Prószyński, 1998
Laufeia Simon, 1889*
Lauharulla Keyserling, 1889?
Lepidemathis Simon, 1883*
Leptathamas Balogh, 1980*
Lophostica Simon, 1902
Maeota Simon, 1901*
Magyarus Żabka, 1985
Maileus Peckham & Peckham, 1907*
Maratus Karsch, 1878*
Margaromma Keyserling, 1882
Marma Simon, 1902*
Mexigonus Edwards, 2003*
Mopiopia Simon, 1902*
Naphrys Edwards, 2003*
Neonella Gertsch, 1936*
Ohilinia Strand, 1911*
Omoedus Thorell, 1881*
Opisthoncana Strand, 1913
Parabathippus Zhang & Maddison, 2012*
Paraharmochirus Szombathy, 1915*
Parasaitis Bryant, 1950
Parvattus Zhang & Maddison, 2012*
Pensacola Peckham & Peckham, 1885*
†*Pensacolatus* Wunderlich, 1988
Pensacolops Bauab, 1983
Petemathis Prószyński & Deeleman-Reinhold, 2012*
Phasmolia Zhang & Maddison, 2012*
Platypsecas Caporiacco, 1955?
Popcornella Zhang & Maddison, 2012*
Pristobaeus Simon, 1902*
Prostheclina Keyserling, 1882*
Pseudemathis Simon, 1902
Pseudeuophrys Dahl, 1912*
Pseudocorythalia Caporiacco, 1938
Rarahu Berland, 1929?
Rhyphelia Simon, 1902
Rumburak Wesolowska, Azarkina & Russell-Smith, 2014*
Saitidops Simon, 1901
Saitis Simon, 1876*
Saitissus Roewer, 1938
Saphrys Zhang & Maddison, 2015*
Semnolius Simon, 1902
Servaea Simon, 1888*
Sidusa Peckham & Peckham, 1895*
Sigytes Simon, 1902
Sobasina Simon, 1898*
Soesilarishius Makhan, 2007*
Spilargis Simon, 1902
Stoidis Simon, 1901
Talavera Peckham & Peckham, 1909*
Tanzania Koçak & Kemal, 2008
Tarodes Pocock, 1899
Thiania C. L. Koch, 1846*
Thorelliola Strand, 1942*
Thyenula Simon, 1902*
Truncattus Zhang & Maddison, 2012*
Tylogonus Simon, 1902*
Udvardya Prószyński, 1992
Variratina Zhang & Maddison, 2012*
Viribestus Zhang & Maddison, 2012*
Viroqua Peckham & Peckham, 1901
Xenocytaea Berry, 1998*
Yacuitella Galiano, 1999?
Yimbulunga Wesolowska, Azarkina & Russell-Smith, 2014
Zabkattus Zhang & Maddison, 2012*

Tribe Salticini (134 species in 7 genera)

Carrhotus Thorell, 1891*
Mogrus Simon, 1882*
Phaulostylus Simon, 1902*
Philaeus Thorell, 1869*
Pignus Wesolowska, 2000*
Salticus Latreille, 1804*
Tusitala Peckham & Peckham, 1902*

Tribe Aelurillini: Subtribe Aelurillina (262 species in 11 genera)

Aelurillus Simon, 1884*
Asianellus Logunov & Heciak, 1996*
Langelurillus Próchniewicz, 1994*
Langona Simon, 1901
Mashonarus Wesolowska & Cumming, 2002
Microheros Wesolowska & Cumming, 1999
Phanuelus Caleb & Mathai, 2015
Phlegra Simon, 1876*
Proszynskiana Logunov, 1996
Rafalus Prószyński, 1999
Stenaelurillus Simon, 1886*

Tribe Aelurillini: Subtribe Freyina (192 species in 26 genera)

Akela Peckham & Peckham, 1896*
Aphirape C. L. Koch, 1850*
Asaracus C. L. Koch, 1846*
Capidava Simon, 1902
Chira Peckham & Peckham, 1896*
Drizztius Edwards, 2015*
Edilemma Ruiz & Brescovit, 2006
Eustiromastix Simon, 1902*
Freya C. L. Koch, 1850*
Frigga C. L. Koch, 1850*
Kalcerrytus Galiano, 2000*
Leptofreya Edwards, 2015
Megafreya Edwards, 2015
Nycerella Galiano, 1982*
Onofre Ruiz & Brescovit, 2007
Pachomius Peckham & Peckham, 1896*
Phiale C. L. Koch, 1846*
Philira Edwards, 2015
Rishaschia Makhan, 2006*
Sumampattus Galiano, 1983
Tarkas Edwards, 2015
Triggella Edwards, 2015
Trydarssus Galiano, 1995*
Tullgrenella Mello-Leitão, 1941
Wedoquella Galiano, 1984
Xanthofreya Edwards, 2015

Tribe Aelurillini: Subtribe Thiratoscirtina (60 species in 14 genera)

Ajaraneola Wesołowska & A. Russell-Smith, 2011?
Alfenus Simon, 1902*
Bacelarella Berland & Millot, 1941*
Cembalea Wesołowska, 1993?
Gramenca Rollard & Wesołowska, 2002?
Lamottella Rollard & Wesołowska, 2002?
Longarenus Simon, 1903*
Malloneta Simon, 1902*
Nimbarus Rollard & Wesołowska, 2002?
Pochyta Simon, 1901*
Saraina Wanless & Clark, 1975*
Tarne Simon, 1886*
Thiratoscirtus Simon, 1886*
Ureta Wesołowska & Haddad, 2013?

Tribe Plexippini: Subtribe Plexippina (493 species in 32 genera)

Afrobeata Caporiacco, 1941
Anarrhotus Simon, 1902*
Artabrus Simon, 1902
Baryphas Simon, 1902*
Brancus Simon, 1902*
Burmattus Prószyński, 1992*
Dasycyptus Simon, 1902?
Dexippus Thorell, 1891
Encymachus Simon, 1902?
Epeus Peckham & Peckham, 1886*
Erasinus Simon, 1899
Evarcha Simon, 1902*
Hermotinus Simon, 1903*
Hyllus C. L. Koch, 1846*
Nigorella Wesołowska & Tomasiewicz, 2008*
Pachyonomastus Caporiacco, 1947
Pancorius Simon, 1902*
Parajotus Peckham & Peckham, 1903?
Paraplexippus Franganillo, 1930?
Pharacocerus Simon, 1902?
Plexippoides Prószyński, 1984*
Plexippus C. L. Koch, 1846*
Polenus Simon, 1902*
Pseudamycus Simon, 1885
Pseudoplexippus Caporiacco, 1947
Ptocasius Simon, 1885*
Schenkelia Lessert, 1927*
Taivala Peckham & Peckham, 1907
Telamonia Thorell, 1887*
Thyene Simon, 1885*
Vailimia Kammerer, 2006
Yaginumaella Prószyński, 1979*

Tribe Plexippini: Subtribe Harmochirina (287 species in 15 genera)

Bianor Peckham & Peckham, 1886*
Eburneana Wesołowska & Szűts, 2001*
Habronattus F. O. P.-Cambridge, 1901*
Harmochirus Simon, 1885*
Havaika Prószyński, 2002*
Iranattus Prószyński, 1992
Microbianor Logunov, 2000
Modunda Simon, 1901
Monomotapa Wesołowska, 2000
Napoca Simon, 1901
Neaetha Simon, 1884
Paraneaetha Denis, 1947
Pellenes Simon, 1876*
Pellolessertia Strand, 1929
Sibianor Logunov, 2001

Salticinae *incertae sedis* (124 species in 48 genera)

Africa

Bokokius Roewer, 1942
Cavillator Wesołowska, 2000
Giuiria Strand, 1906
Hasarinella Wesołowska, 2012
Homalattus White, 1841
Maltecora Simon, 1910
Pachypoessa Simon, 1902
Poessa Simon, 1902
Salpesia Simon, 1901
Simaethulina Wesołowska, 2012
Thyenillus Simon, 1910
Toticoryx Rollard & Wesołowska, 2002
Yogetor Wesołowska & Russell-Smith, 2000
Zulunigma Wesołowska & Cumming, 2011

Asia

Epidelaxia Simon, 1902
Flacillula Strand, 1932
Gambaquezonia Barrion & Litsinger, 1995
Ghumattus Prószyński, 1992
Heliophanoides Prószyński, 1992
Jajpurattus Prószyński, 1992
Lechia Żabka, 1985
Leuserattus Prószyński & Deeleman-Reinhold, 2012
Ligdus Thorell, 1895
Microhasarius Simon, 1902
Necatia Özdikmen, 2007
Panysinus Simon, 1901
Phausina Simon, 1902
Pilia Simon, 1902
Similaria Prószyński, 1992
Stichius Thorell, 1890
Tamigalesus Żabka, 1988

Australasia/Oceania

Adoxotoma Simon, 1909
Ananeon Richardson, 2013
Aruana Strand, 1911
Grayenulla Żabka, 1992
Hinewaia Żabka & Pollard, 2002
Maddisonia Żabka, 2014
Muziris Simon, 1901
Proszynellus Patoleta & Żabka, 2015
Pseudomaevia Rainbow, 1920
Pseudosynagelides Żabka, 1991
Stergusa Simon, 1889
Tatari Berland, 1938

Americas

Albionella Chickering, 1946
Haplopsecas Caporiacco, 1955
Hisukattus Galiano, 1987
Sarindoides Mello-Leitão, 1922
Udalmella Galiano, 1994

Salticidae *incertae sedis* (13 extant species in 9 genera; 28 fossil species in 13 genera)

Africa

Vatovia Caporiacco, 1940

Australasia/Oceania

Hyctiota Strand, 1911

Asia

Ballognatha Caporiacco, 1935
Ceglusa Thorell, 1895
Dolichoneon Caporiacco, 1935
Thianella Strand, 1907

Americas

Arachnotermes Mello-Leitão, 1928
Clynotoides Mello-Leitão, 1944
Stenodeza Simon, 1900

Fossil Salticidae *incertae sedis* (8 species in 6 genera)

†*Attoides* Brongniart, 1877
†*Descangeles* Wunderlich, 1988
†*Eoattopsis* Gourret, 1887
†*Evagoratus* Zhang, Sun & Zhang, 1994
†*Phlegrata* Wunderlich, 1988
†*Steneattus* Bronn, 1856

Fossil Salticidae *incertae sedis*, not in the Salticinae (20 species in 7 genera)

†*Calilinus* Wunderlich, 2004
†*Cenattus* Petrunkevitch, 1942
†*Distanilinus* Wunderlich, 2004
†*Eolinus* Petrunkevitch, 1942
†*Gorgopsidis* Wunderlich, 2004
†*Microlinus* Wunderlich, 2004
†*Paralinus* Petrunkevitch, 1942

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A molecular phylogeny of bark spiders reveals new species from Africa and Madagascar (Araneae: Araneidae: *Caerostris*)

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Abstract. Bark spiders (genus *Caerostris* Thorell 1868) are important models in biomaterial research due to the remarkable biomechanical properties of the silk of *C. darwini* Kuntner & Agnarsson 2010 and its gigantic web. They also exhibit female gigantism and are promising candidates for coevolutionary research on sexual dimorphism. However, *Caerostris* spiders are taxonomically understudied and the lack of a phylogeny impedes evolutionary research. Using a combination of one mitochondrial and one nuclear marker, we provide the first species-level phylogeny of *Caerostris* including half of its species diversity but dense terminal sampling focusing on new lineages. Our phylogenetic and morphological results provide the evidence for six previously undescribed species: *C. almae* n. sp., *C. bojani* n. sp., *C. pero* n. sp. and *C. wallacei* n. sp., all from Madagascar, *C. linnaeus* n. sp. from Mozambique and *C. tinamaze* n. sp. from the Republic of South Africa.

Keywords: Biomaterial, spider silk, web gigantism, sexual size dimorphism, emasculation

Orb web spiders are model organisms in several fields, from functional morphology and physiology, predator-prey interactions, adaptive evolution, evolution of behavior and phylogeography, to sexual selection and biomaterial research (Coddington 1994; Bond & Opell 1998; Barth 2002; Gillespie 2004; Blackledge et al. 2011; Foelix 2011; Herberstein & Wignall 2011; Agnarsson et al. 2013). The "bark spiders" of the genus *Caerostris* Thorell 1868 are widespread throughout the Old World tropics (Grasshoff 1984) but understudied, and recent studies on *Caerostris* propose this clade as suitable for biomaterial and sexual selection research (Agnarsson et al. 2010; Kuntner & Agnarsson 2010).

The species diversity within this genus is incompletely known with only 12 described species worldwide (World Spider Catalog 2015); likewise, their phylogenetic affinities within the largest orb weaving family, Araneidae, remain controversial (Scharff & Coddington 1997; Kuntner et al. 2008, 2013; but, see Gregorič et al. 2015). Recent studies on *Caerostris* of Madagascar hint at undescribed diversity, with several sympatric species inhabiting single rainforest fragments of Madagascar (Fig. 1). *Caerostris* represents the most striking case of web gigantism with several species building orb webs considerably larger than those of most other spiders (Gregorič et al. 2011a, 2015). As an extreme example, *Caerostris darwini* Kuntner & Agnarsson 2010 utilizes a unique habitat by building its giant web in the air column above streams, rivers and lakes (Kuntner & Agnarsson 2010). *Caerostris darwini* builds orbs of up to 2 m in diameter that are suspended between riverbank vegetation by bridge lines that span up to 25 m (Gregorič et al. 2011a). Furthermore, *C. darwini* webs are made of silk that combines strength and elasticity such that it outperforms all other known spider silks, and even most synthetic fibers, in terms of toughness – the work required to fracture the silk (Agnarsson et al. 2010). *Caerostris* spiders also exhibit extreme sexual size dimorphism (SSD), with large females and small males, and seem to have convergently evolved several enigmatic sexual behaviors connected to SSD, e.g., mate guarding, male-male aggressiveness, genital mutilation, mate plugging, and emasculation (Kuntner et al. 2008, 2015). Thus, comparative research on *Caerostris* spiders could yield important insights. Here we provide new taxonomic and phylogenetic hypotheses that will enable such research.

Molecular phylogenies place *Caerostris* on an early branching lineage of Araneidae (Sensenig et al. 2010; Kuntner et al. 2013; Gregorič et al. 2015), but no species-level phylogeny is available. We here provide the first species-level phylogeny of *Caerostris*, using a mitochondrial and a nuclear genetic marker, including six of the 12 described species plus new species. Grasshoff (1984) revised *Caerostris*, conservatively delimiting species, while high somatic and low genital variability within and among species is evident (Grasshoff 1984; Yin et al. 1997; Jäger 2007). Based on genetic distances, we here show that some *Caerostris* species diagnosed by Grasshoff likely represent species complexes, and describe six new species.

METHODS

Taxonomic sampling.—As ingroups we included six of the twelve currently recognized *Caerostris* species, *C. cowani* Butler 1882, *C. darwini*, *C. extrusa* Butler 1882, *C. mitralis* (Vinson 1863), *C. sexcuspidata* (Fabricius 1793) and *C. sumatrana* Strand 1915, and six new species proposed in this paper, *C. almae*, *C. bojani*, *C. linnaens*, *C. pero*, *C. wallacei* and *C. tinamaze*. Our data set totals 50 *Caerostris* specimens (Appendix 1). As *Caerostris* represents an early araneid split (Gregorič et al. 2015), we used the araneids *Argiope* Audouin 1826 and *Acusilas* Simon 1895, and the zygielline *Zygiella* F.O. Pickard-Cambridge 1902 (sister to all other araneids, Kuntner et al. 2013; Gregorič et al. 2015) as outgroups, and

Figure 1.—*Caerostris* diversity in Africa and Madagascar. A: *C. darwini*, Madagascar; B,C: *C. extrusa*, Madagascar; D: *C. pero* new species, Madagascar; E–H: *C. bojani* new species, Madagascar; I,J: *C. linnaeus* new species, Mozambique; K,L: *C. almae* new species, Madagascar; M: *C. cowani*, Madagascar; N,O: Undetermined subadult *Caerostris* females, Madagascar.

rooted the trees with the nephilid *Nephila* Leach 1815 (Appendix 2).

We use the following museum abbreviations: CAS: California Academy of Sciences, San Francisco, California, U.S.A.; USNM: National Museum of Natural History, Smithsonian Institution, Washington DC, U.S.A.; ZMB: Museum für Naturkunde der Humboldt-Universität zu Berlin, Germany.

Morphological examination and imaging.—We performed all measurements using a Leica M165 C stereomicroscope equipped with a Leica DFC 420C camera through the Leica Application Suite 3.8 (Leica Microsystems, Wetzlar, Germany). We report all measurements in millimeters.

We captured images of external structures and epigynal anatomy using the Visionary Digital imaging system, equipped with a Canon 5D Mark II digital camera and an Infinity K2 microscope with Olympus metallurgical lenses, and we captured the images for later stacking using Adobe Lightroom 4 (Adobe Systems Incorporated, San Jose, CA, USA). We stacked the images using Zerene Stacker (Zerene Systems LLC, Richland, WA, USA) and Helicon Focus (Helicon Soft Ltd.), and further manipulated them in Adobe Photoshop CS4 (Adobe Systems Incorporated, San Jose, CA, USA).

We use the following morphological abbreviations in text and figures: ALE = anterior lateral eyes; AME = anterior

median eyes; BH = basal haematodocha; C = conductor; CB = cymbium; CD = copulatory duct; CO = copulatory opening; E = embolus; ETm = embolus-tegulum membrane; FD = fertilization duct; PME = posterior median eyes; PP = pars pendula; S = spermatheca; SD = sperm duct; ST = subtegulum; T = tegulum.

Molecular procedures.—We isolated DNA from leg muscles using the DNeasy Blood and Tissue Kit (QIAGEN, Venlo, Netherlands) following the protocol for mammals. We amplified the mitochondrial cytochrome c oxidase subunit I (CO1) gene fragment for all specimens, and the nuclear large subunit ribosomal (28S) gene fragment for all but five. All PCR reactions had a total volume of 25 µl and consisted of 13.1 µl dd H_2O, 5 µl 5x PCR buffer "GoTaqFlexi" (Promega), 2.25 µl $MgCl_2$ (25 mM, Promega), 0.15 µl "5U GoTaqFlexi Polimerase" (Promega), 2.5 µl "dNTP Mix" (2µM each, Biotools), 0.5 µl of each forward and reverse 20 µM primers, and 1.5 µl of DNA. We included 0.15 µl of bovine serum albumin (Promega, Fitchburg, Wisconsin; 10mg/ml) to some reactions and accordingly decreased the H_2O volume. We performed the PCR amplifications using a "2720 Thermal Cycler" (Applied Biosystems) and a "Mastercycler® ep" (Eppendorf).

We obtained ~ 1.2 kb fragments of CO1 by using several primer combinations. We used the forward "LCO1490" (GGTCAACAAATCATAAAGATATTGG) (Folmer et al. 1994) with the reverse "C1-N-2776" (aka "Maggy"; GGAT AATCAGAATATCGTCGAGG) (Hedin & Maddison 2001) primers to get the whole fragment. Alternatively, we used several combinations of the forward primers LCO1490, "degenerate LCO1490" (GGTCAACAAATCATAAAGAYAT YGG) (Folmer et al. 1994) and C1-J-2123 (aka "Tom"; GATCGAAATTTTAATACTTCTTTTTTTGA) (Vidergar et al. 2014), with the reverse primers Maggy, "HCO2198" (TAAACTTCAGGGTGACCAAAAAATCA) (Folmer et al. 1994), "degenerate HCO2198" (TAAACTTCAGGGTGACC AAARAAYCA) (Folmer et al. 1994) and "Chelicerate-R2" (GGATGGCCAAAAAATCAAAATAAATG) (Barrett & Hebert 2005). We used a touch up program for the primer combination LCO1490 and C1-N-2776. PCR cycling conditions were 96°C for 10 min, followed by 20 cycles of 94°C for 1.5 min, 48°C–52°C for 2 min, 72°C for 2 min, followed by 15 cycles of 94°C for 1.5 min, 52°C for 1.5 min, 72°C for 2 min, and a final extension period of 72°C for 3 min. Shorter fragments using the two primer pairs were sometimes amplified using PCR conditions 94°C for 2 min, followed by 35 cycles of 94°C for 40 sec, 48°C–52°C for 1 min, 72°C for 1 min, and a final extension period of 72°C for 3 min.

We obtained the ~ 0.8 kb fragments of 28S using the forward 28Sa (GACCCGTCTTGAAACACGGA) (Whiting et al. 1997) and reverse 28S-rd5b (CCACAGCGCCAG TTCTGCTTAC) (Whiting et al. 1997) primers. We amplified the fragments using a touch down program with PCR cycling conditions 94°C for 7 min, followed by 20 cycles of 96°C for 45 sec, 62°C–52°C for 45 sec, 72°C for 1 min, followed by 15 cycles of 96°C for 45 sec, 52°C for 45 sec, 72°C for 1 min, and a final extension period of 72°C for 10 min.

Phylogenetic inference.—We aligned the protein coding CO1 sequences using ClustalW, and the ribosomal gene fragment 28S with the online version of MAFFT v.6 (Katoh & Standley 2013), using secondary structure of RNA information during the alignment process (the Q-INS-i strategy) and other values set to default. Because alignments of the 28S gene fragment contained unequal distributions of indels, we used Gblocks 0.91b to eliminate poorly aligned positions and divergent regions of the alignment in order to make our dataset more suitable for phylogenetic analyses (Talavera & Castresana 2007). We set the options to less stringent, allowing gap positions within final blocks, and less strict flanking positions. Using Mesquite 2.75 (Maddison & Maddison 2013), we concatenated gene fragments into two different matrices: first with the full 2016 bp of data, and the second containing ribosomal genes trimmed using Gblocks, summing up to 1965 bp of data.

We conducted Bayesian inference for all analyses. For both the full and Gblocks-trimmed data sets, we used unlinked models for each gene, and also used unlinked models for each gene and codon position in protein coding genes, resulting in four different analyses: the "full gene partition", "gblocks gene partition", "full codon partition" and "gblocks codon partition". We used jModel Test 2.1.3 (Darriba et al. 2012) implementing the Akaike information criterion to statistically select the best-fit models of nucleotide substitutions. We conducted Bayesian analyses using MrBayes v3.1.2 run remotely at the CIPRES Science Gateway (Miller et al. 2010). For all analyses, we performed two independent runs with four simultaneous Markov Chain Monte Carlo chains, each starting with random starting trees, running for a total of 30 million generations. Using the "sump" command in MrBayes, we summarized the sampled parameters and discarded 25% generations as burnin.

Species delimitation.—We calculated genetic distances in the CO1 barcoding region among *Caerostris* individuals using Mega 6.06 (Tamura et al. 2013). We computed genetic distances using the Kimura 2 parameter (Kimura 1980) because this model represents the standard in DNA barcoding (Čandek & Kuntner 2015). We combined the results of our molecular phylogenies with morphological evidence to delimit species. We examined 401 *Caerostris* specimens, encompassing 9 of 12 described species, and only failed to obtain specimens of the Madagascan *C. ecclesigera* Butler 1882 and *C. hirsuta* (Simon 1895), and of *C. mayottensis* Grasshoff 1984 from the Comoros. Among the examined materials, we examined type specimens of *C. amanica* Strand 1907 (junior synonym of *C. vicina*), *C. insularis* Strand 1913 (junior synonym of *C. sexcuspidata*), *C. sumatrana*, and *C. rugosa* Karsch 1878 and *C. petersi* Karsch 1878 (both junior synonyms of *C. mitralis*). In addition to molecular distinction, the newly described species distinctly differ in genital morphology from all previously known species, according to diagnoses of Grasshoff (1984) and Kuntner & Agnarsson (2010). Additionally, we conservatively opted to not split certain widespread clades, despite geographical molecular structuring (e.g., *C. sumatrana* and *C. sexcuspidata*), due to limited specimen sampling outside Madagascar and South Africa (see Discussion).

RESULTS

All analyses strongly supported the monophyly of African *Caerostris* (Fig. 2, Supplemental material 1 [Online at http://

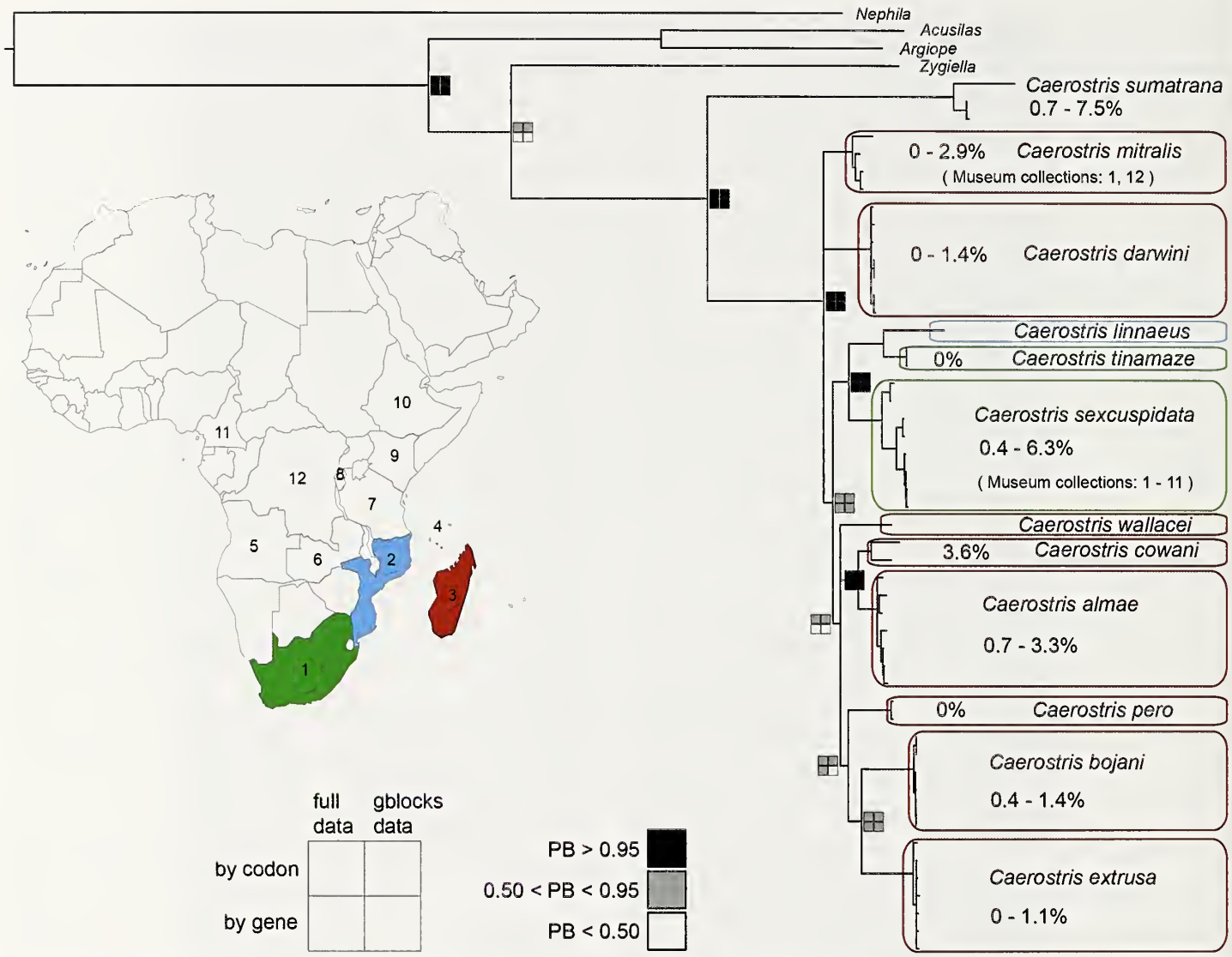

Figure 2.—Summary *Caerostris* phylogeny (full data partitioned by codon), with DNA barcode distances for species. The colored clouds enclosing species show the distribution of sequenced specimens, while the numbered countries show the distribution of species as inferred from museum collections.

dx.doi.org/10.1636/B15-05.s1]). Species from mainland Africa were recovered as monophyletic and nested within Malagasy species, but with weak support. Madagascan *Caerostris*, in turn, were never recovered as monophyletic (Fig. 2, Supplemental material 1 [Online at http://dx.doi.org/10.1636/B15-05.s1]).

The genetic distances among *Caerostris* species inferred from DNA barcodes ranged from 2.88% to 19.8% (ME = 7.43%, IQR = 2.36%). The median intraspecific genetic distance across all investigated *Caerostris* species was 1.25 ± 3.2%. However, *C. sumatrana* and *C. sexcuspidata* likely represent species complexes and the median intraspecific genetic distance excluding these was 1.07 ± 1.67% (see Tables 1 & 2 for species details).

DISCUSSION

We present here the first species level phylogeny of *Caerostris* and describe six new species based on morphological and molecular diagnosability. DNA barcodes have proven to be a generally useful tool to aid species delimitation (Hebert et al. 2003, 2004; Barrett & Hebert 2005; Hajibabaei et al. 2006; Smit et al. 2013; but see Taylor & Harris 2012; Hamilton et al. 2014). This holds true in spiders where DNA barcodes have aided taxonomic decisions (Barrett & Hebert 2005; Arnedo & Ferrández 2007; Longhorn et al. 2007; Blagoev et al. 2009; Kuntner & Agnarsson 2011; Hendrixson et al. 2013; Agnarsson et al. 2015), and offer efficient means of species identification with 90% to 100% accuracy (Čandek & Kuntner 2015). In a sample of Araneidae, the interspecific and intraspecific genetic distances in the barcoding region were found to be 8.8 ± 4.2% and 1.1 ± 1.8%, respectively (Čandek & Kuntner 2015), and the *Caerostris* species investigated here are close to araneid averages (interspecific 7.4 ± 2.4%, intraspecific 1.1 ± 1.7%). The newly described *Caerostris* species are genetically distinct, and are also clearly morphologically diagnosable, further justifying species hypotheses. However, while all species named here are diagnosable by morphology, molecular data imply the existence of further "cryptic species". For example, based on DNA barcodes, *C. ahnae*, *C. bojani*, *C. darwini* and *C. extrusa* are well defined

Table 1.—DNA barcode distances among individuals across the investigated *Caerostris* species.

Species	Range	ME ± IQR
C. almae (N = 7)	0.71–3.275	1.434±1.27
C. bojani (N = 6)	0–1.434	1.072±1.07
C. cowani (N = 2)	3.622	3.622
C. darwini (N = 7)	0–1.43	1.069±0.36
C. extrusa (N = 7)	0–1.427	0.710±0.54
C. mitralis (N = 4)	0–2.9	1.981±2.09
C. pero (N = 2)	0	0
C. sexcuspidata (N = 8)	0.354–6.292	4.007±4.27
C. sumatrana (N = 3)	0.712–7.52	6.717
C. tinamaze (N = 2)	0	0

species with genetic distances among species far exceeding that within species (average 7.4% vs ~ 1%; Tables 1, 2). On the other hand, *C. sexcuspidata* and *C. sumatrana* show intraspecific geographical genetic structuring (average/max. of 4%/6.3% and 6.7%/7.5%, respectively; Tables 1, 2). However, these genetic clusters cannot be morphologically diagnosed with the limited specimens available at present. Furthermore, species delimitation might be influenced by an incomplete or biased sampling, and by population level processes (Hamilton et al. 2014). Thus, further molecular, ecological and biogeographical data are necessary to test whether these lineages represent genetically structured populations or "cryptic" species complexes.

Relationships among species from mainland Africa are not fully resolved, but together they form a strongly supported clade, likely nested among Madagascan species. As we obtained molecular data for 12 of the now 18 known *Caerostris* species, the recovered monophyly of African *Caerostris* is preliminary, but quite likely to persist given the morphological resemblance of African species. Only two *Caerostris* species are currently recognized in Asia, *C. sumatrana* occurring from India to Indonesia, and *C. indica* Strand 1915 known only from Myanmar (Grasshoff 1984; World Spider Catalog 2015). The Asian *Caerostris* we sampled have been identified as *C. sumatrana* based on genital morphology. However, the genetic distance among specimens from South China and Laos reach 7.5% suggesting that broader geographical sampling across Asia will reveal even higher genetic structuring. Similarly, while museum material of *C. sexcuspidata* suggests a wide distribution across southern Africa (Fig. 2; Appendix 1), our results show "intraspecific" genetic distances of 6.3% within South Africa alone. Furthermore, museum material of "*C. sexcuspidata*" from Madagascar are in fact misidentified *C. darwini*. Both *C. sexcuspidata* and *C. sumatrana* as currently circumscribed therefore represent species complexes, and further sampling needs to test this assertion. No fewer than five *Caerostris* species inhabit a single forest fragment in Eastern Madagascar (*C. darwini*, *C. almae*, *C. bojani*, *C. pero* and *C. wallacei*) and this further indicates that *Caerostris* is much more diverse than hitherto appreciated.

Bark spiders are diverse and widespread throughout the Old World tropics. They range from fairly small to large in size, are sexually size dimorphic (Grasshoff 1984), make large to gigantic webs utilizing tough silks, and several species occupy different microhabitats even within small forest fragments (Gregorič et al. 2011a). Thus this charismatic genus offers ample opportunities for evolutionary research. For example, larger orb weaving species in general produce tougher silk, where web architecture and silk material properties coevolve with body size, improving web energy absorbing potential (Sensenig et al. 2010). Also, within individual size classes of species, orb webs undergo compensatory evolution of web performance where silk quality trades off with web architecture and the amount of silk used, a coevolutionary pattern not clearly demonstrated in many other common biomaterials such as byssal threads, tendon and keratin (Sensenig et al. 2010; Blackledge et al. 2012). The evolution of web size and material properties reaches extremes in *Caerostris*, and *C. darwini* represents an extreme in the compensatory evolution of web performance (Sensenig et al. 2010; Gregorič et al. 2015). Furthermore, *C. darwini* web biology strengthens the evidence for coevolution of silk mechanics with ecological and behavioral traits (Gregorič et al. 2011b). Because *Caerostris* species level phylogeny has been lacking, the origin and evolutionary mechanisms shaping web gigantism and silk mechanics remain ambiguous. Our species level *Caerostris*

Table 2.—Average DNA barcode distances among the investigated *Caerostris* species.

DNA barcode distance (%)	*C. almae*	*C. bojani*	*C. cowani*	*C. darwini*	*C. extrusa*	*C. mitralis*	*C. pero*	*C. linnaeus*	*C. wallacei*	*C. sexcuspidata*	*C. sumatrana*
C. bojani	6.4										
C. cowani	4.8	6.5									
C. darwini	6.8	7.9	4.9								
C. extrusa	6.3	6.4	6.4	6.6							
C. mitralis	4.6	8.5	5.3	6.5	6.0						
C. pero	6.7	7.5	7.2	8.0	7.4	6.8					
C. linnaeus	10.2	8.6	8.8	8.9	8.3	8.5	8.6				
C. wallacei	7.3	9.6	7.1	8.5	9.8	8.9	9.4	13.5			
C. sexcuspidata	7.5	9.3	7.4	7.3	7.0	6.2	8.7	8.2	10.6		
C. sumatrana	18.0	18.3	17.9	19.0	17.0	15.7	17.1	18.3	18.8	17.1	
C. tinamaze	9.5	9.5	8.8	10.1	8.7	7.1	9	7.5	13.6	9.8	18.7

phylogeny thus represents a first step towards developing a platform for understanding the evolution of extraordinary biomaterials.

Beyond web and silk evolution research, *Caerostris* may provide a promising additional clade to the more established model spider clades in studies of sexual dimorphism and related biologies (Cheng & Kuntner 2014, 2015; Kuntner & Elgar 2014). Sexual size dimorphism in araneoid spiders may predictably coevolve with behaviors such as emasculation, genital plugging and sexual cannibalism, judging from their convergent co-occurrence in the families Theridiidae, Nephilidae and Araneidae (Kuntner et al. 2015). The first species level phylogeny of *Caerostris* represents a new clade to complement ongoing work on the evolutionary patterns, causes and consequences of SSD in the spider family Nephilidae (Kralj-Fišer et al. 2011; Zhang et al. 2011; Danielson-Francois et al. 2012; Kuntner et al. 2012; Li et al. 2012; Kuntner & Elgar 2014), the araneid *Argiope* (Nessler et al. 2007; Foellmer 2008; Cheng & Kuntner 2014) and the theridiid *Latrodectus* Walckenaer 1805 (Andrade 1996; Kasumovic & Andrade 2009; Modanu et al. 2013).

TAXONOMY

Family Araneidae Clerck 1757
Genus *Caerostris* Thorell 1868 (bark spiders)
(Figs. 1, 3–10)

Aranea: Fabricius 1793: 427, description of *Aranea sexcuspidata* (= *Caerostris sexcuspidata*).

Epeira: Walckenaer, 1805: 67, description of *Epeira imperialis* (= *Caerostris sexcuspidata*).

Gasteracantha: C. L. Koch 1837: 36, description of *Gasteracantha sexcuspidata* (= *Caerostris sexcuspidata*).

Eurysoma: C. L. Koch 1850: 9, description of *Eurysoma sexcuspidata* (= *Caerostris sexcuspidata*).

Caerostris Thorell 1868: 4, 7, 8.

Trichocharis Simon 1895: 835, description of *Trichocharis hirsuta* (= *Caerostris hirsuta*).

Type species.—*Epeira mitralis* Vinson 1863, designated by Thorell 1868: 4.

Diagnosis.—*Caerostris* of both sexes differ from other araneids by the following combination of somatic features: prosoma and opisthosoma wider than long, head region wide and elevated from thoracic region, two pairs of median prosomal projections (none or one pair in males), the sternal tubercule adjacent to coxae IV, the median and lateral eyes grouped on separate tubercules, a frontal rostrum, cheliceral furrow smooth rather than denticulated, the abdominal sigillae, the flattened and hairy patellae, tibiae and metatarsi of legs I, II and IV, the spatulate setae on femur IV, and the ventro-lateral abdominal sclerotization in several rather than one line of small dots (Grasshoff 1984; Kuntner et al. 2008; Kuntner & Agnarsson 2010). *Caerostris* differ from other araneids by the following genital features: female epigynum with paired epigynal hooks (Figs. 3–5, 7–10), male palp with subtegulum of exaggerated size, cymbial ectal margin sclerotized as cymbium rather than transparent, no paracymbium (Kuntner et al. 2008; Kuntner & Agnarsson 2010). *Caerostris* differ from the Zygiellinae, a group sister to all other araneids (Gregorič et al. 2015), by a hairy carapace and extensive rows of hairs on the carapace edge, the posterior eye row procurved rather than straight or recurved, straight rather than sigmoidal first femora, the abdominal humps and a truncated rather than rounded abdomen tip, abdominal dorso-lateral and dorso-central sclerotizations, the strongly sclerotized area around the book lung spiracle, the extensive rather than sparse PMS aciniform field, central rather than peripheral PLS mesal cylindrical gland spigot position, and by distal aggregate spigots embracing flagelliform spigots. *Caerostris* differ from most araneids but not zygiellines by the sustentaculum being parallel to other setae rather than divergent (Kuntner et al. 2008).

Caerostris almae Gregorič new species
(Figs. 1K–L, 3, 4)

Types.—Female holotype deposited at CAS, and labeled: *Caerostris almae* CAE301, Ranomafana NP, Madagascar; Gregorič, Agnarsson, Kuntner 2010. Male paratype deposited at CAS, and labeled: *Caerostris almae* CAE347, Analamazaotra, Madagascar; Griswold, Saucedo, Wood 2009.

Etymology.—The species epithet, a noun in genitive case, honors the first author's mother Alma Gregorič.

Diagnosis.—As in *C. extrusa*, *C. mitralis* (Grasshoff 1984: 19, 20, 29, 30), *C. tinamaze* (Fig. 9C) and *C. wallacei* (Fig. 10C), and in contrast to other *Caerostris* species, the epigynal hooks in *C. almae* (Figs. 3D; 4D, F) are short rather than long, positioned medially on the epigynal plate rather than anteriorly and pointing laterally rather than posteriorly. *C. almae* and *C. mitralis* differ from the above mentioned *Caerostris* species by the posterior epigynal margin that circles around the copulatory openings, and *C. almae* differs from *C. mitralis* by the relatively larger and bulkier epigynal hooks (Figs. 3D; 4D, F; 9C; 10C; Grasshoff 1984: 19, 20). Male *C. almae* differs from other *Caerostris* species by the relatively larger palpal bulbus, and the large and blunt conductor (Fig. 3I–K).

Description.—*Female* (Fig. 3A–E): Total length 10.1. *Prosoma* 4.8 long, 5.8 wide, 4.2 high. Carapace orange to brown, chelicerae dark reddish brown, both covered with white setae. Sternum 2.5 long, 3.2 wide, widest between second leg coxae, light brownish red with white setae in the center. AME diameter 0.2, PME diameter 0.22, AME separation 0.42, PME separation 0.86, PME–PLE separation 2.49, ALE–PLE separation 0.04. Clypeus height 0.43. *Appendages.* Palps brown. Coxae, trochanters and femora of legs orange, femora distally darkened, and patellae, tibiae, metatarsi and tarsi light to dark reddish brown, light brownish annulated. Leg I femur 5.2, patella 3.2, tibia 4.3, metatarsus 4.8, tarsus 1.8. *Opisthosoma* 7.8 long, 8.7 wide, 4.4 high. Base dorsum color light brown and largely covered in dark brown to dark green, with two large pointy light brown tubercules and several small tubercules. Venter brown, black in the middle, with two white transverse bands that end in bright white specks. *Epigynum* as diagnosed (Figs. 3D; 4D, F), spermathecae spheroid (Figs. 3 E; 4E, G).

Male (CAE347 from Analamazaotra, Madagascar, Fig. 3 F–K): Total length 2.8. Prosoma 2.1 long, 1.5 wide, 1 high. Carapace orange brown to reddish brown, chelicerae dark reddish brown, both covered with white setae. Sternum 0.7

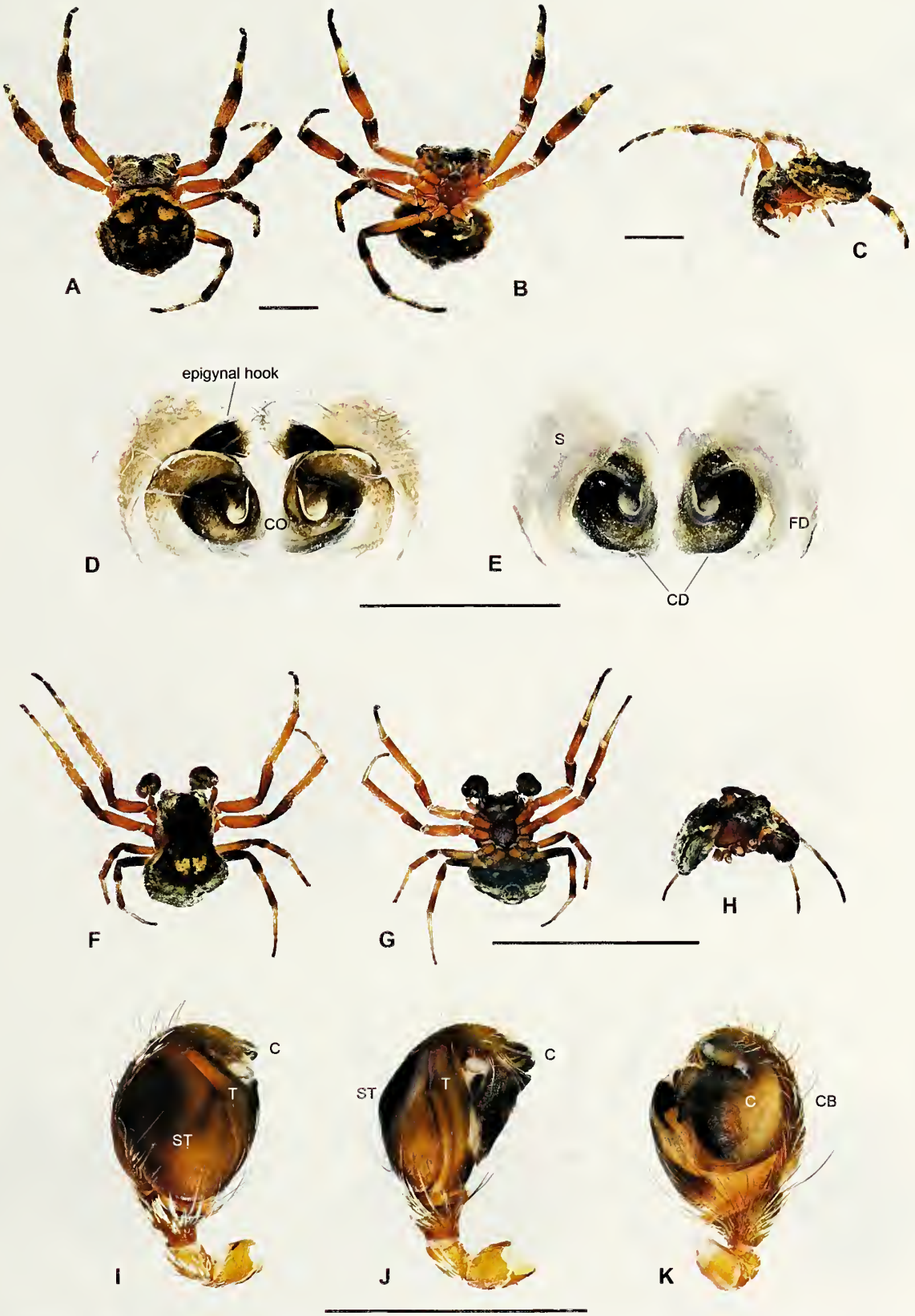

Figure 3.—*Caerostris almae*, female (A–E: CAE301) and male (F–K: CAE347) somatic and genital morphology. D: Female epigynum, ventral; E: Same, dorsal; I: Male right palp, lateral; J: Same, mesal; K: Same, ventral. Somatic scale bars = 5 mm, genital scale bars = 1 mm.

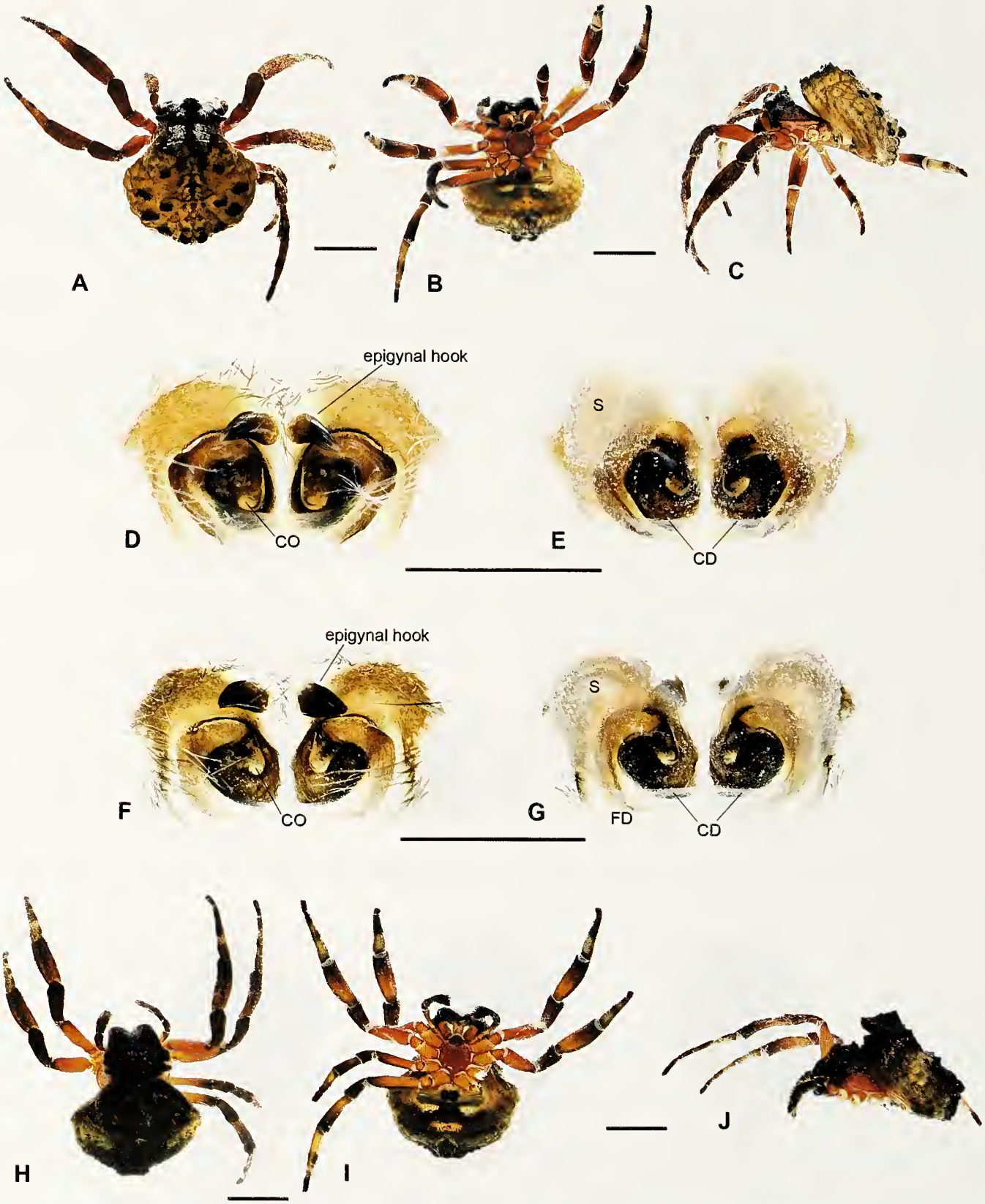

Figure 4.—*Caerostris almae*, female somatic and genital morphology, both from Andasibe-Mantadia, Madagascar. A–C: Female CAE305 somatic morphology; D: Female CAE305 epigynum, ventral; E: Same, dorsal; F: Female CAE303 epigynum, ventral; G: Same, dorsal; H–J: Female CAE303 somatic morphology. Somatic scale bars = 5 mm, genital scale bars = 1 mm.

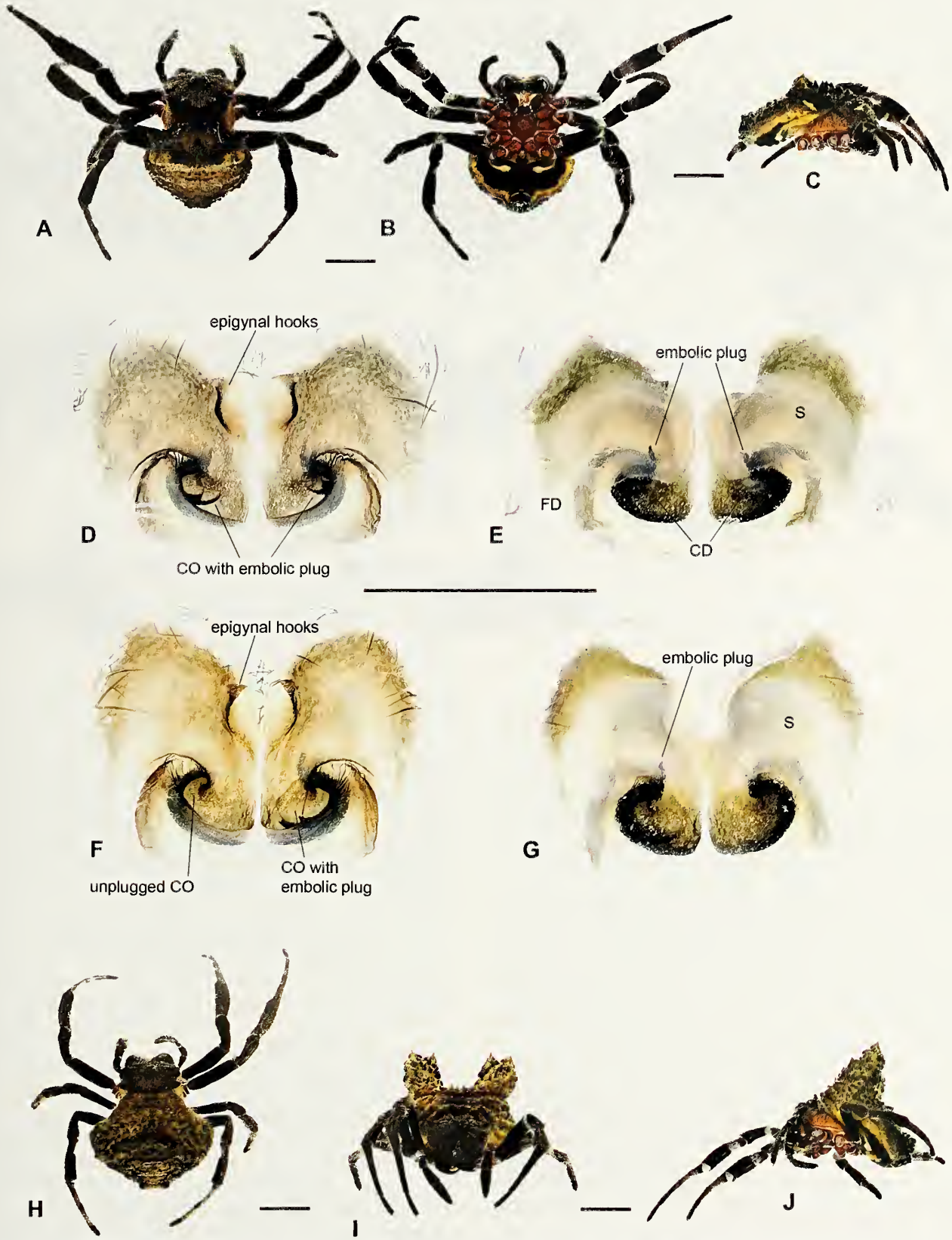

Figure 5.—*Caerostris bojani*, female somatic and genital morphology, all from Andasibe-Mantadia, Madagascar. A–C: Female CAE254 somatic morphology; D: Female CAE254 epigynum, ventral; E: Same, dorsal; F: Female CAE255 epigynum, ventral; E: Same, dorsal; H–J: Female CAE255 somatic morphology. Somatic scale bars = 5 mm, genital scale bar = 1 mm.

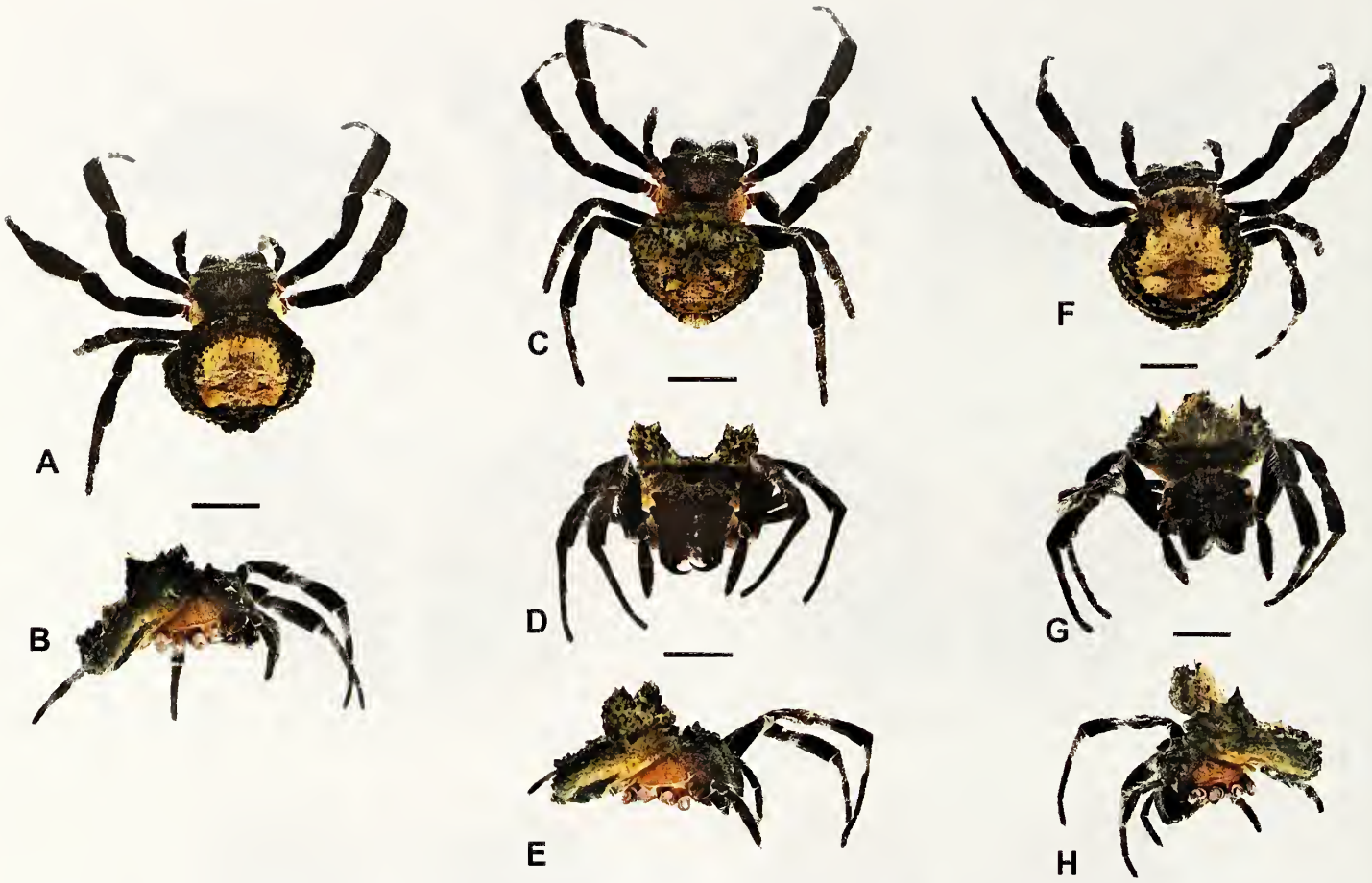

Figure 6.—*Caerostris bojani*, female somatic morphology, all from Andasibe-Mantadia, Madagascar. A, B: CAE263; C–E: CAE262; F–H: CAE252. Somatic scale bars = 5 mm.

long, 0.7 wide, widest between second leg coxae, reddish brown with white setae in the center. AME diameter 0.15, PME diameter 0.1, AME separation 0.16, PME separation 0.42, PME–PLE separation 0.91, ALE–PLE separation 0.03. Clypeus height 0.52. *Appendages*. Palps brown. Coxae, trochanters and femora of legs I and II orange brown to orange. Coxae, trochanters and femora of legs III and IV brown. Femora distally darkened, patellae, tibiae, metatarsi and tarsi light to dark reddish brown. Leg I femur 1.0, patella 1.0, tibia 1.4, metatarsus 1.5, tarsus 0.6. *Opisthosoma* 2.1 long, 2.1 wide, 1 high. Base dorsum color brown and largely covered in dark green with a pair of whitish specks anteriorly. Venter greenish brown. *Palp* as diagnosed (Fig. 3I–K).

Variation.—*Female:* Total length 8.4–13.1; prosoma length 3.9–5.2. Base color of opisthosoma dorsum light brown to brown, sometimes light grey, and covered with dark brown to dark green and black coloration, sometimes yellowish in the center, with several large and/or small tubercules. Opisthosoma venter sometimes black with three pairs of white specks, sometimes one transverse white band, sometimes white speck anteriorly to spinnerets (Figs. 3, 4).

Additional material examined.—Ten females collected at several localities in Madagascar (Appendix 1).

Distribution.—Eastern Madagascar, known from Ranomafana NP, Andasibe-Mantadia NP, Razanaka and Analamazaotra, all Toamasina Province, and from Antsirakambiaty, Fianarantsoa Province.

Natural history.—The species inhabits montane rainforests of Eastern Madagascar. All specimens were found at dawn or night, at forest edge close to water. Web typical for *Caerostris*, capture area 0.45 m^2 (Gregorič et al. *in prep*). Of the material investigated here, the specimen CAE398 had an embolic plug in the left copulatory opening, while others had no embolic plugs.

Caerostris bojani Gregorič new species
(Figs. 1E–H, 5, 6)

Types.—Female holotype deposited at USNM, and labeled: *Caerostris bojani* CAE254, Andasibe-Mantadia NP, Madagascar; Gregorič, Agnarsson, Kuntner 2010.

Etymology.—The species epithet, a noun in genitive case, honors the first author's father Bojan Gregorič.

Diagnosis.—As in *C. pero* (Fig. 8E, G), *C. linnaeus* (Fig. 7C) and *C. mayottensis* (Grasshoff 1984: 37), and in contrast to all other *Caerostris* species, the epigynal hooks in *C. bojani* (Fig. 5D, F) are short rather than long and positioned anteriorly on the epigynal plate rather than medially. *C. bojani* differs from *C. pero*, *C. linnaeus* and *C. mayottensis* by the short epigynal hooks with a wide rather than narrow base, and from *C. mayottensis* by the posterior epigynal margin not circling around the copulatory openings (Figs. 5D, F; 7C; 8E, G; Grasshoff 1984: 37).

Description.—*Female* (CAE254 from Andasibe-Mantadia NP, Madagascar, Fig. 5): Total length 14.8. *Prosoma* 7.6 long,

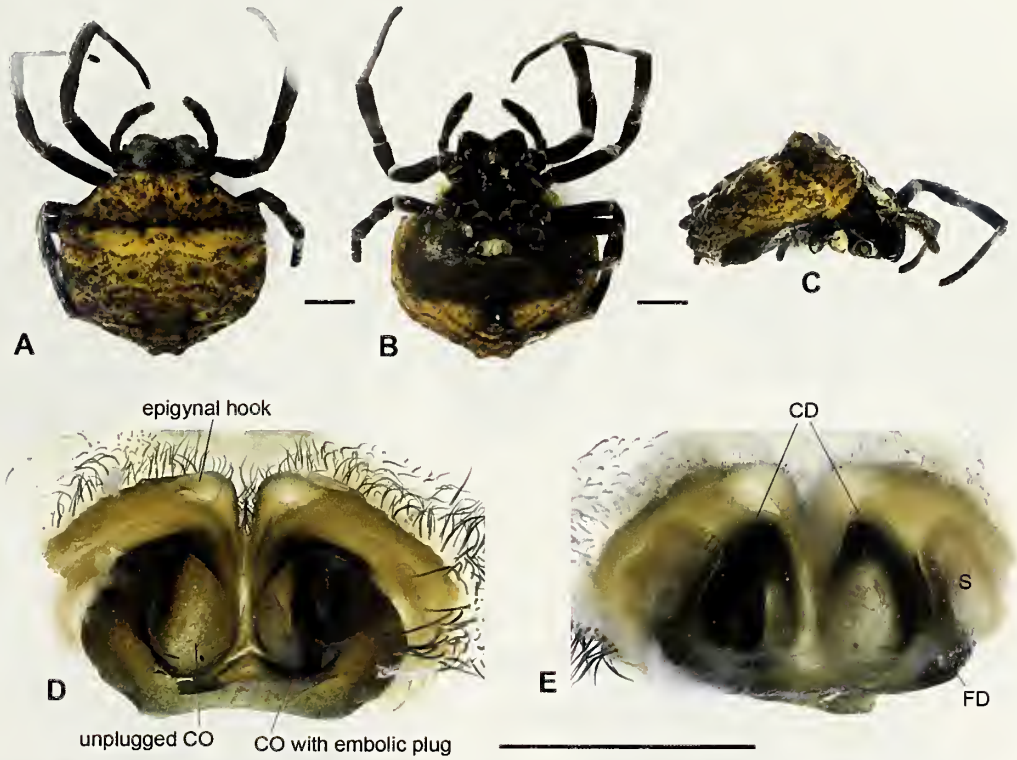

Figure 7.—*Caerostris linnaeus*, female ARA784 somatic and genital morphology, all from Maputo, Mozambique. A–C: Female somatic morphology; D: Female epigynum, ventral; E: Same, dorsal. Somatic scale bar = 5 mm, genital scale bar = 1 mm.

7.8 wide, 6 high. Carapace and chelicerae dark reddish brown, covered with light brown setae. Sternum 3.1 long, 3.1 wide, widest between second leg coxae, brownish red with white setae in the center. AME diameter 0.39, PME diameter 0.33, AME separation 0.44, PME separation 1.17, PME–PLE separation 3.05, ALE–PLE separation 0.08. Clypeus height 0.83. *Appendages*. Palps dark reddish brown. Coxae and trochanters ventrally brownish red. Femora black, patellae, tibiae, metatarsi and tarsi dark brown, ventrally annulated with white hair. Leg I femur 7.1, patella 4.1, tibia 5.6, metatarsus 7.25, tarsus 2.2. *Opisthosoma* 11.3 long, 11.3 wide, 6.3 high. Base color of dorsum grey and brown, covered with dark brown and black spots, with two larger and several smaller tubercules on anterior half. Venter black, outlined with a yellowish brown band, two white transverse bands. *Epigynum* as diagnosed (Fig. 5D), spermathecae kidney-shaped (Fig. 5E).

Variation.—*Female:* Total length 13.2–14.8; prosoma length 5.6–7.6. Opisthosoma grey with greenish tint to brown in color, median dorsum sometimes light brown. Dorsum with several small tubercules, or with a small to big pair of anterior tubercules (Figs. 1E–H, 5, 6).

Additional material examined.—Fifteen females collected in Andasibe-Mantadia NP, Madagascar (Appendix 1).

Distribution.—Known only from the type locality.

Natural history.—The species inhabits mountain rainforests of Eastern Madagascar. It builds its webs at dawn, under closed canopy, and hides on vegetation without web during the day. Web typical for *Caerostris*, capture area 0.16 ± 0.1 m^2 (Gregorič et al. 2011a). Eleven of 15 examined females had their genitals plugged with male embolic parts, eight of these in both copulatory openings.

Caerostris linnaeus Gregorič new species
(Figs. 1I–J, 7)

Types.—Female holotype deposited at USNM, and labeled: *Caerostris linnaeus* ARA784, Maputo, Mozambique; Agnarsson, Kuntner 2013.

Etymology.—The species epithet, a noun in apposition, honors the Swedish biologist and physician Carl Linnaeus.

Diagnosis.—As in *C. bojani* (Fig. 5D, F), *C. mayottensis* (Grasshoff 1984: 37) and *C. pero* (Fig. 8E, G), and in contrast to all other *Caerostris* species, the epigynal hooks in *C. linnaeus* (Fig. 7C) are short rather than long and positioned anteriorly on the epigynal plate rather than medially. *C. linnaeus* differs from *C. mayottensis* by the posterior epigynal margin not circling around the copulatory openings, and from *C. bojani* by the short epigynal hooks with a narrow rather than wide base (Figs. 5D, F; 7C; Grasshoff 1984: 37). *C. linnaeus* differs from *C. pero* by the arch- rather than S-shaped copulatory ducts (Figs. 7D, 8F, H).

Description.—*Female* (ARA784 from Maputo, Mozambique, Fig. 7): Total length 20.7. *Prosoma* 8.9 long, 9 wide, 5.9 high. Carapace and chelicerae dark brown, covered with light brown setae. Sternum 4 long, 3.6 wide, widest between second leg coxae, uniform dark brown. AME diameter 0.34, PME diameter 0.32, AME separation 0.44, PME separation 0.99, PME–PLE separation 3.06, ALE–PLE separation 0.14. Clypeus height 1.03. *Appendages*. Palps brown. Coxae, trochanters and femora dark brown. Patellae, tibiae, metatarsi and tarsi dorsally covered with white hair, tibiae, metatarsi and tarsi ventrally annulated with white hair. Leg I femur 8, patella 4.9, tibia 6.6, metatarsus 7.6, tarsus 2.5. *Opisthosoma* 18.5 long, 20.2 wide, 9.5 high. Base color of dorsum light

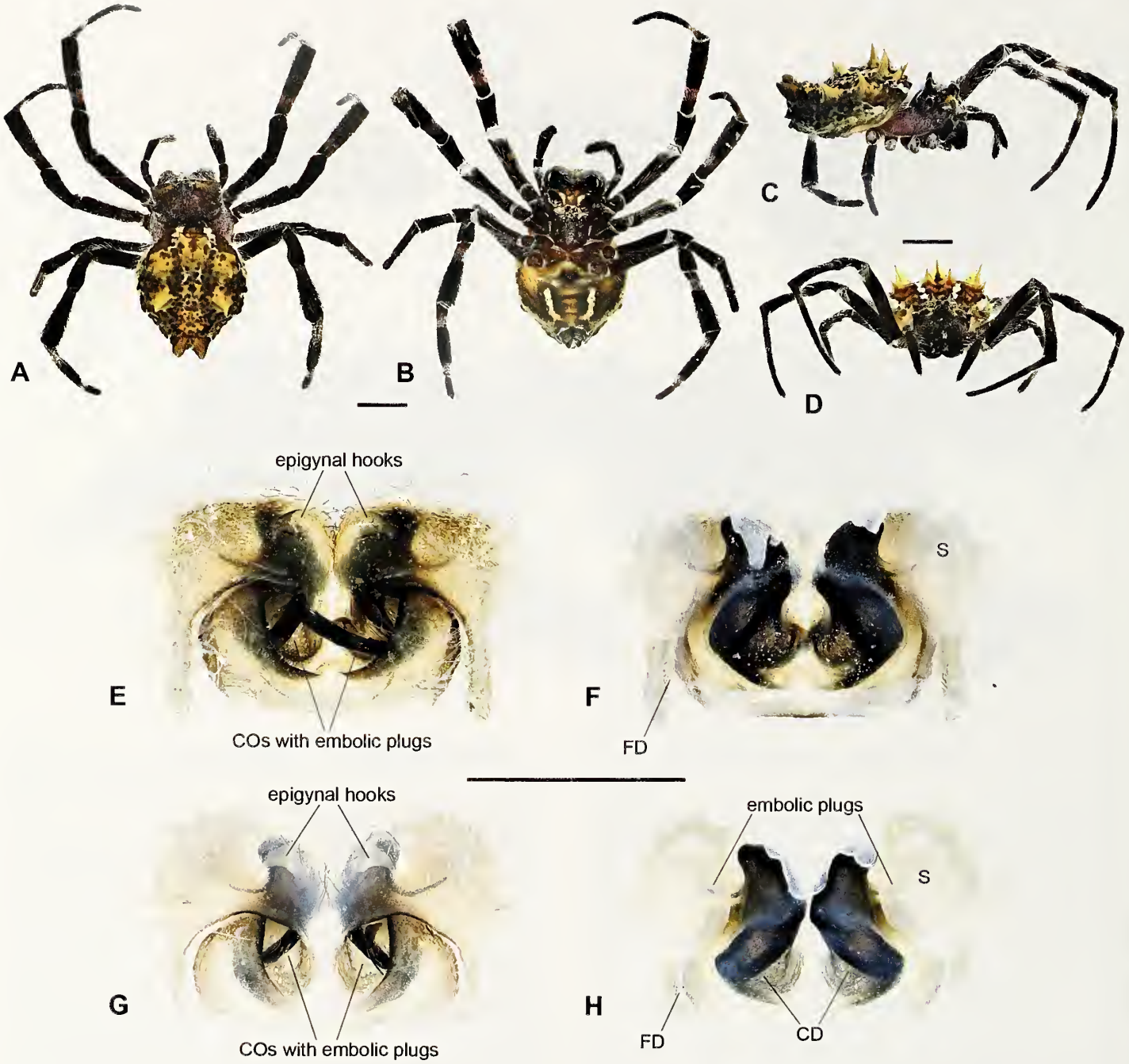

Figure 8.—*Caerostris pero*, female somatic and genital morphology, Andasibe-Mantadia NP, Madagascar. A–C: Female CAE216 somatic morphology; D: Female CAE215 somatic morphology; E: Female CAE215 epigynum, ventral; F: Same, dorsal; G: Female CAE216 epigynum, ventral; H: Same, dorsal. Somatic scale bars = 5 mm, genital scale bar = 1 mm.

brown to yellowish brown, covered with dark brown speeks, with two larger and several smaller tubercules on anterior half. Venter dark brown. *Epigynum* as diagnosed (Fig. 7C), spermathecae kidney-shaped (Fig. 7D).

Variation.—Unknown.

Additional material examined.—None.

Distribution.—South Mozambique, known only from the type locality.

Natural history.—The examined specimen inhabited a forest edge around Maputo, Mozambique. The web typical for the genus *Caerostris*, more than a meter in diameter. The examined female plugged with male embolic parts in the left copulatory opening.

Caerostris pero Gregorič new species
(Figs. 1D; 8)

Types.—Female holotype deposited at USNM, and labeled: *Caerostris pero* CAE215, Andasibe-Mantadia NP, Madagascar; Gregorič, Agnarsson, Kuntner 2010.

Etymology.—The species epithet, a noun in apposition, honors the first author's brother Peter "Pero" Gregorič.

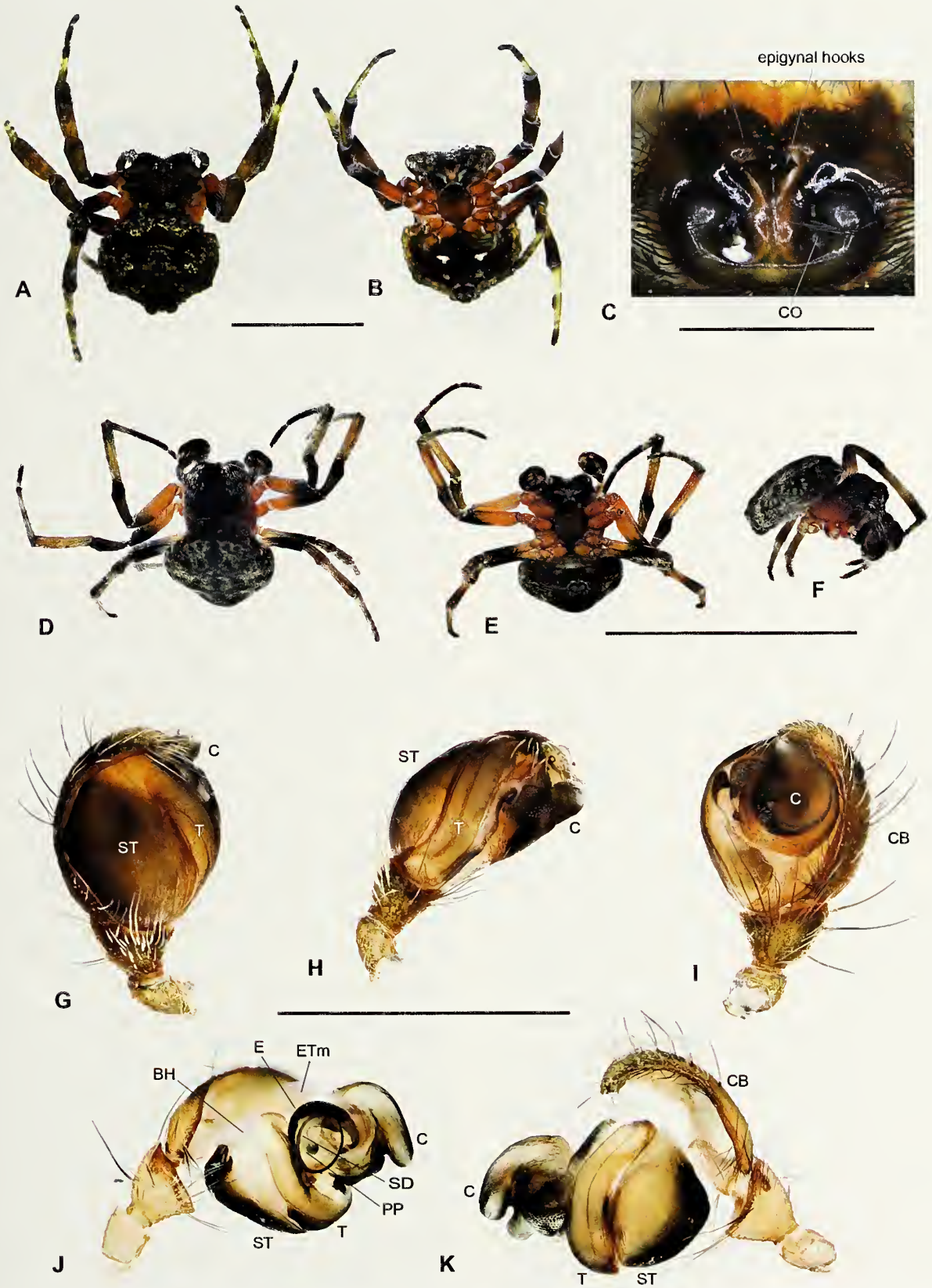

Figure 9.—*Caerostris tinamaze*, female (A–C: CAE341) and male (D–K: CAE341) somatic and genital morphology, Entabeni NR, Republic of South Africa. C: Female epigynum, ventral. G: Male right palp, lateral; H: Same, mesal; I: Same, ventral; J: Male right palp, expanded, mesal; K: Same, ventral. Somatic scale bars = 5 mm, genital scale bars = 1 mm.

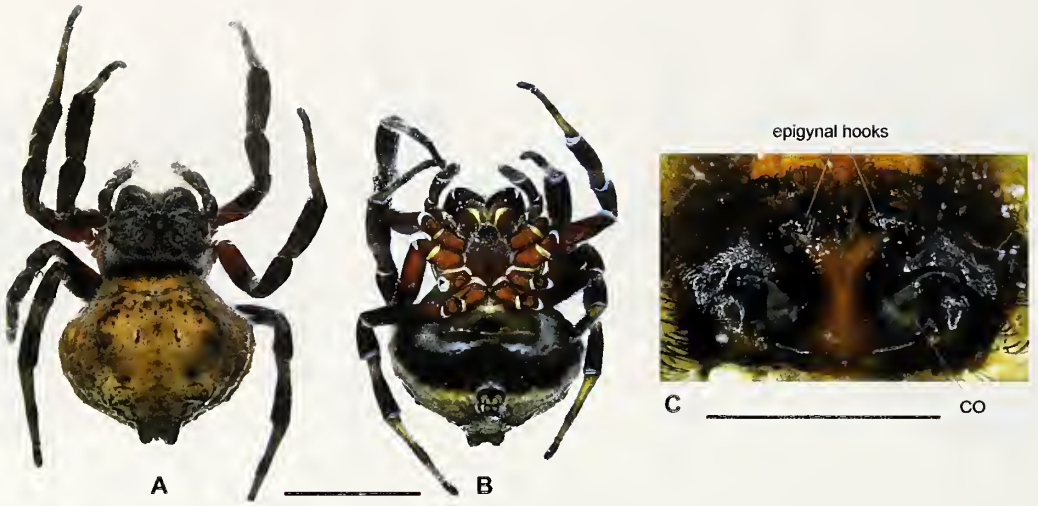

Figure 10.—*Caerostris wallacei*, female CAE334 somatic and genital morphology, Kirindy, Madagascar. C: Female epigynum, ventral. Somatic scale bars = 5 mm, genital scale bar = 1 mm.

Diagnosis.—*Caerostris pero* differs in somatic morphology from all other *Caerostris* species by the 11 pointy tubercules on the opisthosoma dorsum (Fig. 8A, C, D). As in *C. bojani* (Fig. 5D, F), *C. linnaens* (Fig. 7C) and *C. mayottensis* (Grasshoff 1984: 37), and in contrast to all other *Caerostris* species, the epigynal hooks in *C. pero* (Fig. 8E, G) are short rather than long and positioned anteriorly on the epigynal plate rather than medially. *C. pero* differs from *C. mayottensis* by the posterior epigynal margin not circling around the copulatory openings, from *C. bojani* by the short epigynal hooks with a narrow rather than wide base (Figs. 5D, F; 8E, G; Grasshoff 1984: 37), and from *C. linnaeus* by the S- rather than arch-shaped copulatory ducts (Figs. 7D, 8F, H).

Description.—*Female* (CAE215 from Andasibe-Mantadia NP, Madagascar, Fig. 8): Total length 16.4. *Prosoma* 6.6 long, 6.9 wide, 3.1 high. Carapace and chelicerae dark reddish brown, covered with white setae. Sternum 2.5 long, 3.2 wide, widest between second leg coxae, dark reddish brown with white setae longitudinally in the center. AME diameter 0.34, PME diameter 0.27, AME separation 0.41, PME separation 0.76, PME–PLE separation 2.25, ALE–PLE separation 0.27. Clypeus height 0.82. *Appendages*. Palps dark reddish brown. Legs dorsally dark brown, light brownish annulated. Coxae, trochanters and femora of legs I and II ventrally reddish brown, patellae, tibiae, metatarsi and tarsi ventrally dark brown. Coxae and trochanters of legs III and IV ventrally brown, femora ventrally reddish brown, patellae, tibiae, metatarsi and tarsi ventrally dark brown. Leg I femur 8.5, patella 6.1, tibia 6, metatarsus 7.2, tarsus 2.3. *Opisthosoma* 13.2 long, 10.9 wide, 4 high. Dorsum brown covered with dark brown spots, with light brown longitudinal band, with 11 pointy light brown tubercles. Venter brown with two narrow, white median longitudinal bands. *Epigynum* as diagnosed (Fig. 8E), spermathecae spheroid (Fig. 8F).

Variation.—*Female:* Total length 14.3–18.6; prosoma length 5.8–6.7.

Additional material examined.—Eighteen females collected in Andasibe-Mantadia NP, Madagascar (Appendix 1).

Distribution.—Eastern Madagascar, known only from the type locality.

Natural history.—The species inhabits montane rainforests of Eastern Madagascar. It suspends its large orb web in the air column over small forest streams under closed canopy. Web typical for *Caerostris*, capture area 0.48 ± 0.21 m^2 (Gregorič et al. 2011a). Ten of the 18 examined females had their genitals plugged with male embolic parts, five of these in both copulatory openings.

Caerostris tinamaze Gregorič new species
(Fig. 9)

Types.—Female holotype and male paratype deposited at CAS, and labeled: *Caerostris tinamaze* CAE341, Entabeni NR, Republic of South Africa; Miller, Wood 2006.

Etymology.—The species epithet, a noun in apposition, honors the Slovenian alpine skiing champion Tina Maze.

Diagnosis.—As in *C. extrusa*, *C. mitralis* (Grasshoff 1984: 19, 20, 29, 30), *C. almae* (Figs. 3D; 4D, F) and *C. wallacei* (Fig. 10C), and in contrast to other *Caerostris* species, the epigynal hooks in *C. tinamaze* (Fig. 9C) are short rather than long, positioned medially on the epigynal plate rather than anteriorly and pointing laterally rather than posteriorly. *C. tinamaze* differs from *C. almae* and *C. mitralis* by the posterior epigynal margin not circling around the copulatory openings (Figs. 3D; 4D, F; 9C; 10C; Grasshoff 1984: 19, 20, 29, 30). *C. tinamaze* differs from *C. sexcuspidata* by the laterally pointing epigynal hooks (Fig. 9C; Grasshoff 1984: 16, 17). Male *C. tinamaze* differs from other *Caerostris* by the blunt and anteriorly pointing conductor.

Description.—*Female* (CAE341 from Entabeni NR, Limpopo province, Republic of South Africa, Fig. 9A–C): Total length 9. *Prosoma* 4.3 long, 4.6 wide, 3.8 high. Carapace and chelicerae brown, covered with light brown setae. Sternum 2.1 long, 2.3 wide, widest between second leg coxae, orange. AME diameter 0.21, PME diameter 0.22, AME separation 0.38, PME separation 0.72, PME–PLE separation 1.77, ALE–PLE separation 0.05. Clypeus height 0.55. *Appendages*. Palps greenish brown. Coxae and trochanters orange. Femora

orange in proximal half and black in distal half. Patellae and tibiae dorsally greenish brown, and ventrally brown with annulation of yellowish brown pigment and white setae. Metatarsi proximally pale yellowish and dark brown distally, tarsi brown. Leg I femur 4.2, patella 2.6, tibia 3.6, metatarsus 4.3, tarsus 1.7. *Opisthosoma* 7 long, 7.1 wide, 3.7 high. Dorsum greenish brown with several small tubercules. Venter outlined with light brown, median black with two pairs of white specks. *Epigynum* as diagnosed (Fig. 9C), spermathecae unknown.

Male (CAE341 from Entabeni NR, Madagascar, Fig. 9D–K): Total length 2.9. Prosoma 1.6 long, 1.5 wide, 1 high. Carapace reddish brown to brown, chelicerae dark reddish brown, both covered with white setae. Sternum 0.8 long, 0.8 wide, widest between second leg coxae, brown. AME diameter 0.11, PME diameter 0.13, AME separation 0.16, PME separation 0.37, PME–PLE separation 0.47, ALE–PLE separation 0.07. Clypeus height 0.2. *Appendages*. Palps brown. Coxae, trochanters and femora of legs I and II orange brown. Coxae, trochanters and femora of legs III and IV brown. Femora distally darkened, patellae, tibiae, metatarsi and tarsi light to dark brown. Metatarsi and tarsi of leg I almost entirely black. Leg I femur 1.3, patella 0.81, tibia 1.3, metatarsus 1.2, tarsus 0.5. *Opisthosoma* 2.1 long, 2.3 wide, 1 high. Base dorsum color dark brown and largely covered in dark green. Venter dark brown to black. *Palp* as diagnosed (Fig. 9G–K).

Variation.—Unknown.

Additional material examined.—None.

Distribution.—Known only from the type locality.

Natural history.—The examined specimens inhabited an afromontane forest fragment in a pine plantation. The examined female was plugged with male embolic parts in the right copulatory opening, the examined male intact.

Caerostris wallacei new species
(Fig. 10)

Types.—Female holotype deposited at CAS, and labeled: *Caerostris wallacei* CAE334, Kirindy, Madagascar; Wood, Miller 2006.

Etymology.—The species epithet, a noun in genitive case, honors the "other father" of evolutionary biology, Alfred R. Wallace.

Diagnosis.—As in *C. extrusa*, *C. mitralis* (Grasshoff 1984: 19, 20, 29, 30), *C. almae* (Figs. 3D; 4D, F) and *C. tinamaze* (Fig. 9C), and in contrast to other *Caerostris* species, the epigynal hooks in *C. wallacei* (Fig. 10C) are short rather than long, positioned medially on the epigynal plate rather than anteriorly and pointing laterally rather than posteriorly. *C. wallacei* differs from *C. almae* and *C. mitralis* by the posterior epigynal margin not circling around the copulatory openings, and from *C. extrusa* and *C. tinamaze* by bulky and straight epigynal hooks (Figs. 3D; 4D, F; 9C; 10C: Grasshoff 1984: 19, 20, 29, 30).

Description.—*Female* (CAE334 from Kirindy, Toliara, Madagascar, Fig. 10): Total length 15.9. *Prosoma* 6.5 long, 7.3 wide, 5.6 high. Carapace and chelicerae brown, covered with white and yellowish setae. Sternum 3 long, 3.1 wide, widest between second leg coxae, orange. AME diameter 0.26, PME diameter 0.26, AME separation 0.53, PME separation 1.09, PME–PLE separation 2.61, ALE–PLE separation 0.11. Clypeus height 0.76. *Appendages*. Palps brown. Coxae and trochanters orange. Femora ventrally I–II orange, distally dark brown, greyish dorsally. Femora III–IV orange proximally, dark brown distally, greyish dorsally. Patellae brown, greyish dorsally. Tibiae brown, light and annulated with white setae proximally, greyish dorsally. Metatarsi yellowish ventrally and greyish dorsally. Tarsi brown. Leg I femur 5.7, patella 3.5, tibia 4.5, metatarsus 5.9, tarsus 1.9. *Opisthosoma* 12.1 long, 12.3 wide, 7.8 high. Dorsum yellowish brown, with several small tubercules and sclerotized dots. Venter brown. *Epigynum* as diagnosed (Fig. 10C).

Variation.—Unknown.

Additional material examined.—None.

Distribution.—Southern Madagascar, known only from the type locality.

Natural history.—The type specimen inhabited the dry deciduous Kirindy forest of Southern Madagascar. The examined female genitals were not plugged with male embolic parts.

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APPENDICES

Appendix 1.—Taxonomic and distribution information of the *Caerostris* material examined in this study: information for specimens of each species is given as the database code, sex and number, and locality details.

Caerostris almae

CAE301, 1 female, Madagascar, Ranomafana, elev. 1000 m, 21.256514S 47.437372E, 22.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE303, 1 female, Madagascar, Ranomafana, elev. 1000 m, 21.256514S 47.437372E, 19.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE305, 1 female, Madagascar, Andasibe-Mantadia NP, elev. 900-1000 m, 18.937172S 48.420053E, 7.-8.v.2001, Agnarsson I., Kuntner M.

CAE337, 2 female, Madagascar, Antsirakambiaty, elev. 1550 m, 20.594S 46.564E, 22-26.i.2003, Griswold C., Fisher

CAE338, 1 female, Madagascar, Analamazaotra, elev. 960 m, 18.9297167S 48.4116E, 31.i.-3.ii.2009, Griswold C., Saucedo A., Wood H.

CAE347, 1 male, Madagascar, Analamazaotra, elev. 960 m, 18.9297167S 48.4116E, 31.i.-3.ii.2009, Griswold C., Saucedo A., Wood H.

CAE399, 1 female, Madagascar, Andasibe-Mantadia NP, elev. 900-1000 m, 18.937172S 48.420053E, 8.iii.-21. iv. 2012, Gregorič M., Cheng R.C., Šuen K.

Caerostris bojani

CAE252, 1 female, Madagascar, Andasibe-Mantadia NP, elev. 900-1000 m, 18.937172S 48.420053E, 8.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE253, 1 female, Madagascar, Andasibe-Mantadia NP, elev. 900-1000 m, 18.937172S 48.420053E, 8.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE254, 1 female, Madagascar, Andasibe-Mantadia NP, elev. 900-1000 m, 18.937172S 48.420053E, 7.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE255, 1 female, Madagascar, Andasibe-Mantadia NP, elev. 900-1000 m, 18.937172S 48.420053E, 7.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE256, 1 female, Madagascar, Andasibe-Mantadia NP, elev. 900-1000 m, 18.937172S 48.420053E, 12.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE257, 1 female, Madagascar, Andasibe-Mantadia NP, elev. 900-1000 m, 18.937172S 48.420053E, 8.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE258, 1 female, Madagascar, Andasibe-Mantadia NP, elev. 900-1000 m, 18.937172S 48.420053E, 12.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE260, 1 female, Madagascar, Andasibe-Mantadia NP, elev. 900-1000 m, 18.937172S 48.420053E, 8.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE261, 1 female, Madagascar, Andasibe-Mantadia NP, elev. 900-1000 m, 18.937172S 48.420053E, 7.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE262, 1 female, Madagascar, Andasibe-Mantadia NP, elev. 900-1000 m, 18.937172S 48.420053E, 8.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE263, 1 female, Madagascar, Andasibe-Mantadia NP, elev. 900-1000 m, 18.937172S 48.420053E, 7.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE304, 1 female, Madagascar, Andasibe-Mantadia NP, elev. 900-1000 m, 18.937172S 48.420053E, 23.iv.2008, Agnarsson I., Kuntner M.

CAE306, 1 female, Madagascar, Andasibe-Mantadia NP, elev. 900-1000 m, 18.937172S 48.420053E, 7.-8.v.2001, Agnarsson I., Kuntner M.

CAE308, 2 females, Madagascar, Andasibe-Mantadia NP, elev. 900-1000 m, 18.937172S 48.420053E, 7.-8.v.2001, Agnarsson I., Kuntner M.

Caerostris cowani

CAE300, 1 female, Madagascar, Ranomafana, elev. 1000 m, 21.256514S 47.437372E, 19.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE340, 1 female, Madagascar, Ambohitantely, elev. 1620 m, 18.171389S 47.28194E, 19-21.iii.2003, Andriamalala D., Silva D.

Caerostris darwini

CAE233, 1 female, Madagascar, Mantadia, elev. 950 m, 18.783784S 48.427617E, 28.ii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE236, 1 female, Madagascar, Antananarivo, elev. 1280 m, 18.930325S 47.526810E, 25.ii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE270F, 1 female, Madagascar, Madraka private reserve, elev. 1370 m, 18.912647S 47.892627E, 2.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE270M, 1 male, Madagascar, Madraka private reserve, elev. 1370 m, 18.912647S 47.892627E, 2.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE289, 1 female, Madagascar, Andasibe-Mantadia NP, elev. 900-1000 m, 18.9472S 48.418394E, 4.iv.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE294, 1 female, Madagascar, Andasibe-Mantadia NP, elev. 900-1000 m, 18.937172S 48.420053E, 30.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE298, 1 female, Madagascar, Ranomafana, elev. 1000 m, 21.256514S 47.437372E, 22.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

Caerostris extrusa

CAE218, 1 female, Madagascar, Mantadia, elev. 950 m, 18.783784S 48.427617E, 28.ii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE220, 1 female, Madagascar, Mantadia, elev. 950 m, 18.783784S 48.427617E, 28.ii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE221, 1 female, Madagascar, Mantadia, elev. 950 m, 18.783784S 48.427617E, 28.ii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE227, 1 female, Madagascar, Mantadia, elev. 950 m, 18.783784S 48.427617E, 28.ii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE279, 1 female, Madagascar, Ranomafana, elev. 1000 m, 21.256514S 47.437372E, 22.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE281, 1 female, Madagascar, Ranomafana, elev. 1000 m, 21.256514S 47.437372E, 22.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE331, 1 female, Madagascar, Analamazaotra, elev. 960 m, 18.9297167S 48.4116E, 31.i.-3.ii.2009, Griswold C., Saucedo A., Wood H.

Caerostris linnaeus

ARA784, 1 female, Mozambique, Maputo, elev. 30 m, N -25.922183S 32.552909E, Kuntner M., Agnarsson I.

Caerostris nitralis

CAE332, 1 female, Madagascar, Montagne d'Ambre, elev. 1000 m, 12.5234167S 49.1734E, 14.xii.2005, Wood H., Raholiarisendra H., Rabemahafaly J.

CAE333, 1 female, Madagascar, Montagne d'Ambre, elev. 800 m, 12.4713S 49.21283E, 17.xii.2005, Wood H., Raholiarisendra H., Rabemahafaly J.

CAE345F, 1 female, Madagascar, Analalava, elev. 700 m, 22.59167S 45.1283E, 1-5.ii.2003, Griswold C., Fisher

CAE345M, 2 males, Madagascar, Analalava, elev. 700 m, 22.59167S 45.1283E, 1-5.ii.2003, Griswold C., Fisher

Caerostris pero

CAE210, 1 female Madagascar, Mantadia, elev. 950 m, 18.783784S 48.427617E, 26.ii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE212, 1 female Madagascar, Mantadia, elev. 950 m, 18.783784S 48.427617E, 28.ii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE213, 1 female Madagascar, Mantadia, elev. 950 m, 18.783784S 48.427617E, 26.ii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE214, 1 female Madagascar, Mantadia, elev. 950 m, 18.783784S 48.427617E, 26.ii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE215, 1 female Madagascar, Mantadia, elev. 950 m, 18.783784S 48.427617E, 26.ii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE216, 1 female Madagascar, Mantadia, elev. 950 m, 18.783784S 48.427617E, 26.ii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE245, 1 female Madagascar, Andasibe-Mantadia NP, elev. 900-1000m, 18.937172S 48.420053E, 12.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE246, 1 female Madagascar, Andasibe-Mantadia NP, elev. 900-1000m, 18.937172S 48.420053E, 12.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE247, 1 female Madagascar, Andasibe-Mantadia NP, elev. 900-1000m, 18.937172S 48.420053E, 11.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE248, 1 female Madagascar, Mantadia, elev. 950 m, 18.783784S 48.427617E, 26.ii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE249, 1 female Madagascar, Andasibe-Mantadia NP, elev. 900-1000m, 18.937172S 48.420053E, 12.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE250, 1 female Madagascar, Andasibe-Mantadia NP, elev. 900-1000m, 18.937172S 48.420053E, 11.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE251, 1 female Madagascar, Andasibe-Mantadia NP, elev. 900-1000m, 18.937172S 48.420053E, 12.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE266, 1 female Madagascar, Andasibe-Mantadia NP, elev. 900-1000m, 18.937172S 48.420053E, 11.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE267, 1 female Madagascar, Andasibe-Mantadia NP, elev. 900-1000m, 18.937172S 48.420053E, 11.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE268, 1 female Madagascar, Andasibe-Mantadia NP, elev. 900-1000m, 18.937172S 48.420053E, 11.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE269, 1 female Madagascar, Andasibe-Mantadia NP, elev. 900-1000m, 18.937172S 48.420053E, 11.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

CAE397, 1 female Madagascar, Andasibe-Mantadia NP, elev. 900-1000m, 18.937172S 48.420053E, 12.iii.2010, Agnarsson I., Kuntner M., Gregorič M.

Caerostris sexcuspidata

CAE187, 1 female, Tanzania, Mpafu NR, elev. 15 m, 7.283654S 39.349953E, 29.i.2009, Pienke S.

CAE205, 1 female, RS. Africa, Hogsback, elev. 1070 m, 32.60205S 26.944783E, 28.iii.2011, Haddad C.

CAE206, 1 female, RS. Africa, Hogsback, elev. 1070 m, 32.60205S 26.944783E, 28.iii.2011, Haddad C.

CAE207, 1 female, RS. Africa, Hogsback, elev. 1250 m, 32.595483S 26.931567E, 27.iii.2011, Haddad C.

CAE208, 1 female, RS. Africa, Hogsback, elev. 1250 m, 32.595483S 26.931567E, 27.iii.2011, Haddad C.

CAE339, 1 female, RS. Africa, Tsitsikamma National Park, elev. 15 m, 34.023483S 23.8903E, 17-18.ii.2006, Miller J., Wood H.

CAE344F, 1 juvenile female, RS. Africa, Tsitsikamma NP, elev. 15 m, 34.023483S 23.8903E, 17-18.ii.2006, Miller J., Wood H.

CAE344M, 3 males, RS. Africa, Tsitsikamma NP, elev. 15 m, 34.023483S 23.8903E, 17-18.ii.2006, Miller J., Wood H.

Caerostris sumatrana

CAE004, 2 females, Laos, Muong Sing, elev. 640 m, N21.190367S 101.1575E, 3.xi.2004, Jäger P., Vedel V.

CAE203, 1 female, China, Baka, elev. 690 m, N21.713675S 100.783023E, 6.i.2011, Gregorič M., Kuntner M.

CAE204, 1 juvenile female, China, Baka, elev. 690 m, N21.713 675S 100.783023E, 6.i.2011, Gregorič M., Kuntner M.

Caerostris tinamaze

CAE341F, 1 female, RS. Africa, Entabeni NR, elev. 1375 m, 22.9960278S 30.264472E, iii.2006, Miller J., Wood H.

CAE341M, 1 male, RS. Africa, Entabeni NR, elev. 1375 m, 22.9960278S 30.264472E, iii.2006, Miller J., Wood H.

Caerostris wallacei

CAE334, 1 female, Madagascar, Kirindy forest, elev. 50 m, 20.0671S 44.65723E, 20-30.i.2006, Wood H., Miller J.

Appendix 2.—Taxonomic and genetic information about the terminals used in our analyses, with GenBank accession numbers (four 28S accession codes are missing because we lacked the nucleotide data).

Database code	Family	Genus	Species	CO1 acc. code	28S acc. code
	Nephilidae	*Nephila*	*fenestrata*	KC849084	KC849002
	Araneidae	*Zygiella*	*atrica*	KR526594	KR526501
	Araneidae	*Acusilas*	*coccineus*	KR526559	KR526466
	Araneidae	*Argiope*	*argentata*	FJ607554	FJ607519
CAE301	Araneidae	*Caerostris*	*ahnae*	KT267101	KT267150
CAE303	Araneidae	*Caerostris*	*ahnae*	KT267102	KT267151
CAE305	Araneidae	*Caerostris*	*ahnae*	KT267103	
CAE337	Araneidae	*Caerostris*	*ahnae*	KT267104	KT267152
CAE338	Araneidae	*Caerostris*	*ahnae*	KT267105	KT267153
CAE347	Araneidae	*Caerostris*	*ahnae*	KT267106	KT267154
CAE399	Araneidae	*Caerostris*	*ahnae*	KT267107	
CAE252	Araneidae	*Caerostris*	*bojani*	KT267093	KT267143
CAE253	Araneidae	*Caerostris*	*bojani*	KT267094	KT267144
CAE256	Araneidae	*Caerostris*	*bojani*	KT267095	KT267145
CAE257	Araneidae	*Caerostris*	*bojani*	KT267096	KT267146
CAE263	Araneidae	*Caerostris*	*bojani*	KT267097	KT267147
CAE304	Araneidae	*Caerostris*	*bojani*	KT267098	
CAE300	Araneidae	*Caerostris*	*cowani*	KT267064	KT267114
CAE340	Araneidae	*Caerostris*	*cowani*	KT267065	KT267115
CAE233	Araneidae	*Caerostris*	*darwini*	KT267066	KT267116
CAE236	Araneidae	*Caerostris*	*darwini*	KT267067	KT267117
CAE270F	Araneidae	*Caerostris*	*darwini*	KT267068	KT267118
CAE270M	Araneidae	*Caerostris*	*darwini*	KT267069	KT267119
CAE289	Araneidae	*Caerostris*	*darwini*	KT267070	KT267120
CAE294	Araneidae	*Caerostris*	*darwini*	KT267071	KT267121
CAE298	Araneidae	*Caerostris*	*darwini*	KT267072	KT267122
CAE218	Araneidae	*Caerostris*	*extrusa*	KT267073	KT267123
CAE220	Araneidae	*Caerostris*	*extrusa*	KT267074	KT267124
CAE221	Araneidae	*Caerostris*	*extrusa*	KT267075	KT267125
CAE227	Araneidae	*Caerostris*	*extrusa*	KT267076	KT267126
CAE279	Araneidae	*Caerostris*	*extrusa*	KT267077	KT267127
CAE281	Araneidae	*Caerostris*	*extrusa*	KT267078	KT267128
CAE331	Araneidae	*Caerostris*	*extrusa*	KT267079	KT267129
ARA765	Araneidae	*Caerostris*	*linnaeus*	KT267092	KT267142
CAE332	Araneidae	*Caerostris*	*mitralis*	KT267080	KT267130
CAE333	Araneidae	*Caerostris*	*mitralis*	KT267081	KT267131
CAE345F	Araneidae	*Caerostris*	*mitralis*	KT267083	KT267133
CAE345M	Araneidae	*Caerostris*	*mitralis*	KT267082	KT267132
CAE212	Araneidae	*Caerostris*	*pero*	KT267099	KT267148
CAE213	Araneidae	*Caerostris*	*pero*	KT267100	KT267149
CAE187	Araneidae	*Caerostris*	*sexcuspidata*	KT267084	KT267134
CAE205	Araneidae	*Caerostris*	*sexcuspidata*	KT267085	KT267135
CAE206	Araneidae	*Caerostris*	*sexcuspidata*	KT267086	KT267136
CAE207	Araneidae	*Caerostris*	*sexcuspidata*	KT267087	KT267137
CAE208	Araneidae	*Caerostris*	*sexcuspidata*	KT267088	KT267138
CAE339	Araneidae	*Caerostris*	*sexcuspidata*	KT267089	KT267139
CAE344F	Araneidae	*Caerostris*	*sexcuspidata*	KT267091	KT267141
CAE344M	Araneidae	*Caerostris*	*sexcuspidata*	KT267090	KT267140
CAE004	Araneidae	*Caerostris*	*sumatrana*	KT267113	
CAE203	Araneidae	*Caerostris*	*sumatrana*	KT267111	KT267158
CAE204	Araneidae	*Caerostris*	*sumatrana*	KT267112	KT267158
CAE341F	Araneidae	*Caerostris*	*tinamaze*	KT267109	KT267156
CAE341M	Araneidae	*Caerostris*	*tinamaze*	KT267110	KT267157
CAE334	Araneidae	*Caerostris*	*wallacei*	KT267108	KT267155

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On three new *Euathlus* tarantulas from Argentina and cladistic analysis of the genus

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Abstract. Three unknown species of *Euathlus* Ausserer 1875 (Araneae: Theraphosidae) are recognized and formally described. *Euathlus diamante* Ferretti sp. nov., *E. sagei* Ferretti sp. nov., and *E. tenebrarum* Ferretti sp. nov. are described from the Mendoza and Neuquén provinces of western Argentina. The cladistic analysis showed *Euathlus* as monophyletic supported by the following synapomorphies: i) male tibial apophysis with fused branches bases; ii) presence of a ventral spine on retrolateral branch of male tibial apophysis; iii) sternum longer than wide. According to this cladistics analysis, a tree topology of (*Homoeomma uruguayense* (Mello-Leitão 1946) (*Plesiopelma longisternale* (Schiapelli & Gerschman 1942) (*Grammostola anthracina* (C.L. Koch 1842) (*Phrixotrichus scrofa* (Molina 1788) (*E. tenebrarum* sp. nov. (*E. truculentus* L. Koch 1875, *E. sagei* sp. nov. ((*E. parvulus* (Pocock 1903) (*E. condorito* Perafán & Pérez-Miles 2014, *E. manicata* (Simon 1892), *E. atacama* Perafán & Pérez-Miles 2014)) (*E. antai* Perafán & Pérez-Miles 2014, *E. diamante* sp. nov.)))))))) is reported.

Keywords: New species, spider, Theraphosidae, systematics, phylogenetics

Theraphosidae Thorell 1894 is the largest family of mygalomorph spiders with 126 genera and more than 950 species described mainly in tropical and subtropical regions (World Spider Catalog 2014). These spiders show noticeable taxonomic difficulties given their great morphological homogeneity (Raven 1985; Pérez-Miles et al. 1996; Bertani 2000; Perafán & Pérez-Miles 2014). An example of that is the genus *Euathlus* Ausserer 1875, which has experienced a long and controversial taxonomic history, evidenced by the difficulties of diagnosing and differentiating species (Perafán & Pérez-Miles 2014).

Euathlus was established on the basis of its type species *E. truculentus* L. Koch 1875, originally described from Argentina and Chile. Recently, Perafán & Pérez-Miles (2014) made a taxonomic revision and phylogenetic analysis of the genus *Euathlus* describing new species and providing a diagnostic key. However, the authors did not examine additional material from Argentina and consequently, only made reference to the original data of *E. truculentus* (Perafán & Pérez-Miles 2014).

The genus *Euathlus* is characterized by possessing only one patch of urticating setae, and those setae consisting of Type III and Type IV urticating setae. Males have a palpal organ with two prolateral keels and tip directed retrolaterally, the tibial apophyses with retrolateral spines, a subapical spine on retrolateral branch and a basal spine on prolateral branch. Females have two spermathecal receptacles with a lateral spheroid chamber (Perafán & Pérez-Miles 2014). This genus is morphologically similar and phylogenetically related to *Phrixotrichus* Simon 1889 (Perafán & Pérez-Miles 2014). To date, *Euathlus* has six valid species: *Euathlus antai* Perafán & Pérez-Miles 2014, *E. atacama* Perafán & Pérez-Miles 2014, *E. condorito* Perafán & Pérez-Miles 2014, *E. manicata* (Simon 1892), *E. parvulus* (Pocock 1903), all distributed in Chile, and *E. truculentus* L. Koch 1875 from Argentina and Chile.

Investigation of material from the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-Ar) and the Instituto Argentino de Investigaciones de las Zonas Áridas (CAI), along with material recorded in recent survey campaigns (granted by the British Tarantula Society) to the Andean-patagonic forests of south western Argentina (Neuquén province), led me to describe three new species from western Argentina. Moreover, I present a cladistic analysis of *Euathlus* building upon the dataset presented by Perafán & Pérez-Miles (2014) including these new species.

METHODS

The specimens used in this study are lodged in the following institutions: Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza, Argentina (CAI); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires Argentina (MACN-Ar); Laboratorio de Zoología de Invertebrados II, Universidad Nacional del Sur, Buenos Aires, Argentina (LZI). Specimens were examined using an Olympus SZ stereomicroscope and photographed using a SONY Hx200v camera attached to a stereomicroscope. The following abbreviations are utilized: ALE = anterior lateral eyes, AME = anterior median eyes, BN = basal nodule, D = dorsal, P = prolateral, PB = prolateral branch of tibial apophysis, PI = prolateral inferior keel, PLE = posterior lateral eyes, PLS = posterior lateral spinnerets, PME = posterior median eyes, PMS = posterior median spinnerets, PS = prolateral superior keel, R = retrolateral, RB = retrolateral branch of tibial apophysis. Female genitalia were dissected and cleared in concentrated lactic acid for 60–120 minutes to study the shape of spermathecae. All measurements are given in millimeters and were made with digital dial calipers with an error of 0.01mm, rounded up to one significant decimal where appropriate and an Olympus stereoscopic microscope equipped with an ocular micrometer scale. Appendage measurements were based on left appendages in the dorsal view. Lengths of leg articles were taken from the mid-proximal point of articulation to the mid-distal point of the article (*sensu* Coyle (1995) Fig. 1 and Bond (2012) Figs. 11–16). Terminology for tibial apophyses (or spurs) follows the general usage in Theraphosidae. It includes the prolateral apophysis (or apophysis branch) and retrolateral apophysis (e.g., Bertani 2001; Pérez-Miles et al. 2008). Spine notation follows Petrunkevitch (1925). Male palpal bulb keels terminology follows Bertani (2000). Urticating setae terminology follows Cooke et al. (1972).

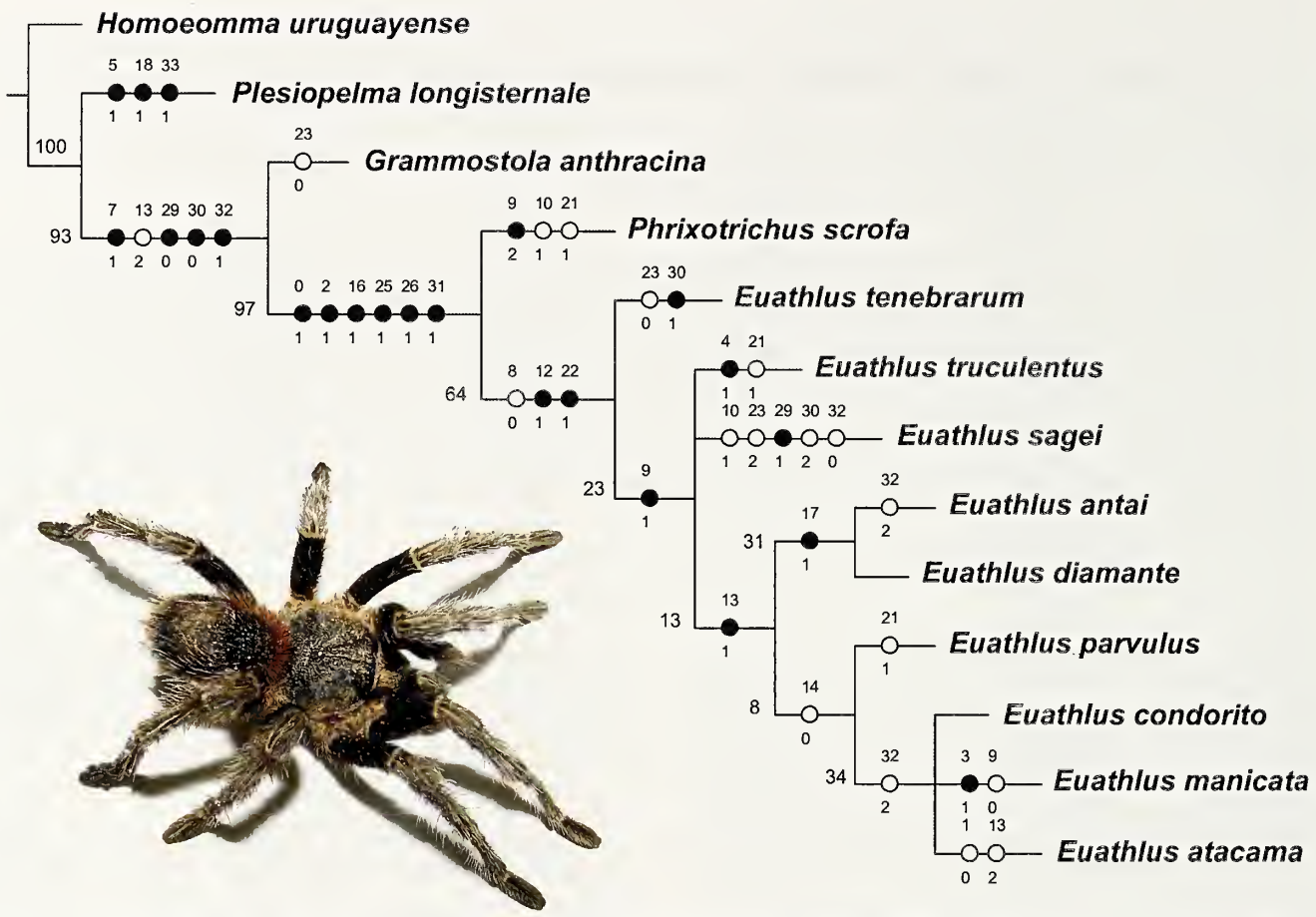

Figure 1.—Hypothetical *Euathlus* phylogenetic relationships. One tree using implicit enumeration (Length = 59; CI = 0.71; RI = 0.66). White and black circles imply homoplastic and non-homoplastic characters that define each node, respectively. The numbers at each node are the frequency differences (GC) jackknife values.

Cladistic analysis built upon the data matrix from Pérez-Miles & Perafán (2014).—I scored the newly described species (*Euathlus diamante* sp. nov., *Euathlus sagei* sp. nov. and *Euathlus tenebrarum* sp. nov.) for 34 characters (Table 1) obtained from Perafán & Pérez-Miles (2014), removing invariant characters. The ingroup comprised nine taxa: *Euathlus antai*, *E. atacama*, *E. condorito*, *E. diamante* sp. nov., *E. manicata*, *E. parvulus*, *E. sagei* sp. nov., *E. tenebrarum* sp. nov., and *E. truculentus*. The outgroup used and their character scores were taken from Perafán & Pérez-Miles (2014). The outgroup included the following species: *Homoeomma uruguayense* (Mello-Leitão 1946); *Grammostola anthracina* (C.L. Koch 1842); *Phrixotrichus scrofa* (Molina 1788); and *Plesiopelma longisternale* (Schiapelli & Gerschman 1942). The tree was rooted using *H. uruguayense*. The data matrix was constructed using Nexus Data Editor version 0.5.0 software (Page 2001). Parameters used in this study followed Perafán & Pérez-Miles (2014), allowing a more explicitly comparison of results between the two studies. For that purpose, the cladistic analysis was carried out with the program TNT version 1.1 (Goloboff et al. 2003a), using the implicit enumeration algorithm. Implied weighting (Goloboff 1993) was used with concavity indices (k) ranging from 1 to 6. Jacknife (Goloboff et al. 2003b) values were calculated for each node using resampled matrices, with 1000 pseudoreplicates and 36% as the probability of alteration.

Characters scored taken from Perafán & Pérez-Miles (2014).—Multistate characters were coded as non-additive. The data matrix is listed in Table 1. (0) Embolus direction: directed ventrolaterally = 0; directed retrolaterally = 1. (1) Relative width of bulb sclerites II + III: wide = 0; narrow (less than 10% of length) = 1. (2) Position of distal PI: prolateral = 0; prolateroventral = 1. (3) Apical keel: absent = 0; present = 1. (4) Ventral crest on PI: absent = 0; present = 1. (5) Subapical tooth on PI: absent = 0; present = 1. (6) Tegular apophysis on bulb: absent = 0; present = 1. (7) Position of male tibial apophysis: ventral = 0; prolateroventral = 1. (8) Male tibial apophysis: branches with fused bases: 0, branches with non-fused bases: 1. (9) Male tibial apophysis: with one retrolateral spine = 0; with two retrolateral spines = 1; without retrolateral spines = 2. (10) PB: with basal spine = 0; without basal spine = 1. (11) Position of distal spine on RB: subapical = 0; apical = 1. (12) Ventral spine on RB: absent = 0; present = 1. (13) Flexion of male metatarsus I: between the branches of tibial apophysis = 0; on the apex to the retrolateral branch = 1; retrolateral to the tibial apophysis = 2. (14) Male metatarsus I: strongly curved = 0; straight = 1. (15) Spermathecal morphology: spheroid shape = 0; not spheroid shape = 1. (16) Spermathecae with a lateral spheroid chamber: absent = 0; present = 1. (17) Spermathecal receptacles: single = 0; bifurcated = 1. (18) Spermathecal neck: straight = 0; spiralled = 1. (19) Digitiform projections

Table 1.—Character matrix used in cladistic analysis of *Euathlus*. (?) unknown; treated as missing data in the analysis.

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
H. uruguayense	0	0	0	?	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	2	2	1	2	2	2	0	0	0
P. longistemale	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	1	2	2	0	0	1
G. anthracina	0	1	0	0	0	0	0	1	1	0	0	1	0	2	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
P. scrofa	1	1	1	0	0	0	0	1	1	2	1	1	0	2	1	1	1	0	0	0	0	1	0	1	1	1	1	0	0	0	0	1	1	0
E. truculentus	1	1	1	0	1	0	0	1	0	1	0	0	1	2	1	1	1	0	0	0	1	1	1	?	?	1	1	0	0	0	0	1	?	0
E. parvulus	1	1	1	0	0	0	0	1	0	1	0	0	1	1	0	1	1	0	0	0	1	1	1	1	1	1	1	0	0	0	0	1	1	0
E. condorito	1	1	1	0	0	0	0	1	0	1	0	0	1	1	0	1	1	0	0	0	1	0	1	1	1	1	1	0	0	0	0	1	2	0
E. manicata	1	1	1	1	0	0	0	1	0	0	0	0	1	1	0	?	?	?	?	?	?	0	1	1	1	1	1	0	0	0	0	1	2	0
E. atacama	1	0	1	0	0	0	0	1	0	1	0	0	1	2	0	1	1	0	0	0	1	0	1	1	1	1	1	0	0	0	0	1	2	0
E. antai	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	0	0	1	0	1	1	1	1	1	0	0	0	0	1	2	0
E. diamante	1	0	1	0	0	0	0	1	0	1	0	0	1	1	1	1	1	1	0	0	1	0	1	1	1	1	1	0	0	0	0	1	1	0
E. sagei	1	1	1	0	0	0	0	1	0	1	1	0	1	2	1	1	1	0	0	0	1	0	1	2	1	1	1	0	0	1	2	1	0	0
E. tenebrarum	1	1	1	0	0	0	0	1	0	0	0	0	1	2	1	1	1	0	0	0	1	0	1	0	1	1	1	0	0	0	1	1	1	0

on spermathecae: absent = 0; present = 1. (20) Female palpal tibia spination: with apical spines only = 0; with apical and others ventral spines = 1. (21) Labial cuspules: numerous (> 20) = 0; few or none = 1. (22) Sternum: as long as wide = 0; longer than wide = 1. (23) Extension of scopula on metatarsus I: complete = 0; more than a half (distal 2/3) = 1; distal half = 2. (24) Extension of scopula on metatarsus II: more than half (distal 2/3) = 0; distal half = 1. (25) Extension of scopula on metatarsus III: distal half = 0; less than half (1/3) = 1; only apical (1/4, 1/5) = 2. (26) Extension of scopula on metatarsus IV: less than half (1/3) = 0; only apical (1/4, 1/5) = 1; absent = 2. (27) Scopulae on tarsi I: entire = 0; widely divided = 1. (28) Seopulae on tarsi II: entire = 0; narrowly divided = 1; widely divided = 2. (29) Scopulae on tarsi III: entire = 0; narrowly divided = 1; widely divided = 2. (30) Scopulae on tarsi IV: entire = 0; narrowly divided = 1; widely divided = 2. (31) Tarsal claws: with teeth = 0; without teeth = 1. (32) Length of urticating setae type III: short (less than 0.75 of the optical field diameter of microscope; 40×) = 0; medium-sized (more than 0.75 and less than 1.5 of the optical field diameter, 40×) = 1; long (more than 1.5 of the optical field diameter, 40×) = 2. (33) Barbs on urticating setae type III: long = 0; short = 1.

The data matrix obtained from Perafán & Pérez-Miles (2014) comprises 8 continuous quantitative characters and 25 discrete characters. The use of continuous characters has been questioned and may be inappropriate for phylogenetic reconstruction (Hendrixson & Bond 2009). Hendrixson & Bond (2009) indicated that due caution should be exercised before employing this character type mainly in the absence of other independently derived source of characters. Unfortunately, lacking discrete characters is a ubiquitous phenomenon found across the Mygalomorphae, a lineage morphologically homogeneous that clearly lacks rich sources of discrete characters (Hendrixson & Bond 2009). Also, a number of methods for handling these continuous data exist (García-Cruz & Sosa 2006), all with different implications for inferring accurate phylogenies. However, Goloboff et al. (2006) suggested using implied weights (Goloboff 1993), a method implemented in the present work.

PHYLOGENETICS

The phylogenetic analysis using implied weighting and implicit enumeration resulted in a single tree (Fig. 1) with K values from 1 to 6 (59 steps, CI = 0.71, RI = 0.66). The genus *Euathlus* is monophyletic including the new species, supported by the following synapomorphies: male tibial apophysis with fused branches bases (Figs. 2e, 4f, 7e); presence of a ventral spine on retrolateral branch of male tibial apophysis (Figs. 2e, 4f, 7e) and sternum longer than wide (Figs. 2d, 4d, 7d). *Euathlus tenebrarum* sp. nov., characterized by having a complete extension of scopula on metatarsus I and narrowly divided on tarsi IV, was shown to be the sister group to the remaining species by the presence of one retrolateral spine on male tibial apophysis. *Euathlus truculentus* is the sister species to the group of *E. antai*, *E. diamante* sp. nov., *E. parvulus*, *E. condorito*, *E. manicata* and *E. atacama* supported by the flexion of male metatarsus I on the apex to the retrolateral branch. The position of *E. sagei* sp. nov. was unresolved. The monophyletic group of *E. diamante* sp. nov. and *E. antai*

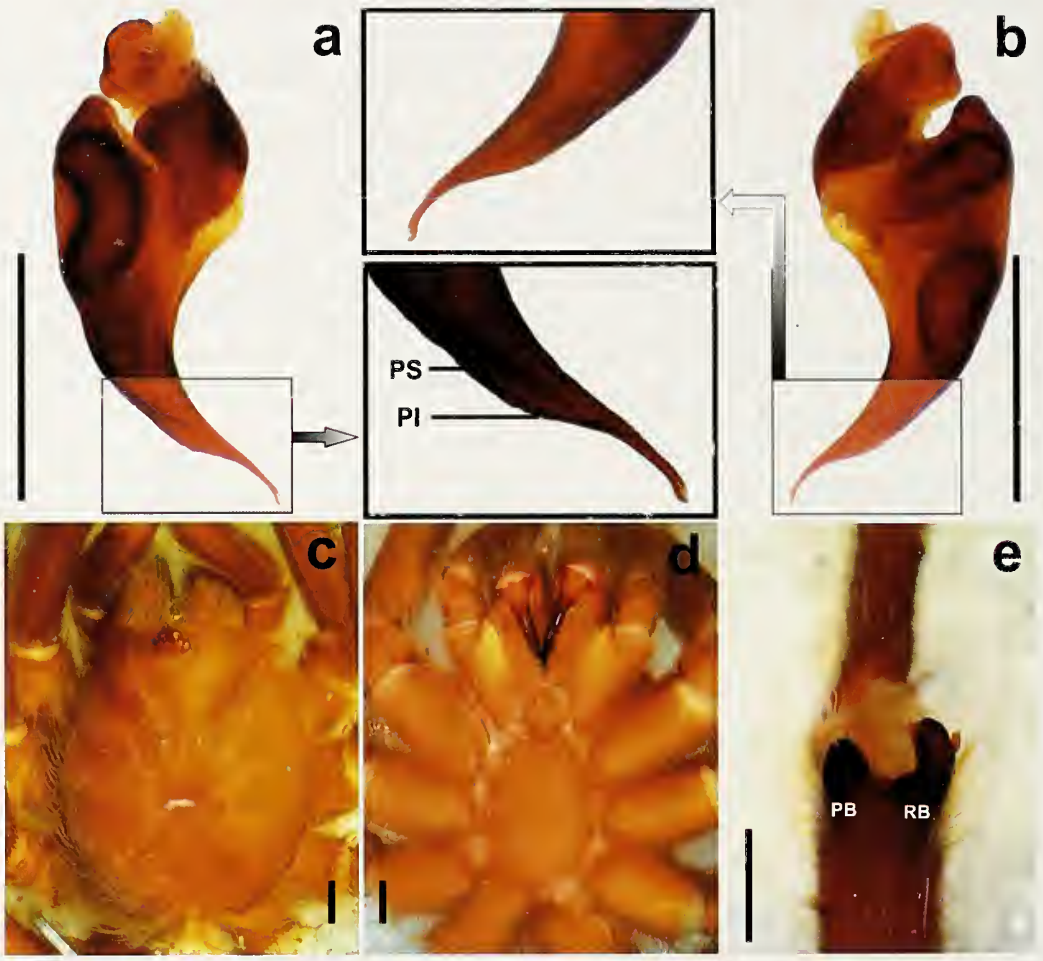

Figure 2.—*Euathlus diamante* sp. nov. male holotype (CAI 3330). a. Palpal organ, prolateral view, the box indicates the apical embolus with keels; b. palpal organ, retrolateral view, the box indicates the apical embolus; c. carapace, dorsal view; d. sternum, ventral view; e. tibial apophysis, ventral view. PS = prolateral superior keel, PI = prolateral inferior keel, PB = prolateral branch, RB = retrolateral branch. Scale bar = 1 mm.

is supported by the bifurcated spermathecal receptacles (Fig. 3e). *Euathlus parvulus* is the sister group of *E. condorito*, *E. manicata* and *E. atacama*, which are together supported by the strongly curved male metatarsus. There were no synapomorphies that resolve the internal relationships within the *parvulus* group, but their monophyly is supported by possession of long urticating setae type III. Perafán & Pérez-Miles (2014) reported on the monophyly of the genus *Euathlus*, and with the inclusion of these new species, the genus continues to be well supported. *Euathlus truculentus* was the sister species of the all remaining *Euathlus* (Perafán & Pérez-Miles 2014), but in the present work, *Euathlus tenebrarum* sp. nov. is determined to be the sister lineage to all other *Euathlus*. The position of *Euathlus parvulus* is similar to that found by Perafán & Pérez-Miles (2014). Moreover, *E. antai* was found to be the sister species of *E. diamante* sp. nov., a relationship unresolved in the phylogeny proposed by Perafán & Pérez-Miles (2014).

TAXONOMY

Family Theraphosidae Thorell 1870

Genus *Euathlus* Ausserer 1875

Euathlus diamante new species

Figs. 2 & 3, Tables 2 & 3

Type material.—Male holotype: ARGENTINA: *Mendoza*: San Carlos department, Reserva Laguna de Diamante, Alvarado (34.2439° S, 69.3778° W), elevation 2297 m, 5–8 January 2006, S. Roig & G. Debandi (CAI 3330). Female paratype: ARGENTINA: *Mendoza*: San Carlos department, Reserva Laguna de Diamante, Alvarado (34.2350° S, 69.3833° W), elevation 2347 m, 13–23 February 2006, S. Claver & R. Carrara (CAI 3317).

Etymology.—The name refers to the Diamante Volcano in Mendoza, Argentina, where this species was found.

Diagnosis.—Male of this species can be distinguished by the non-convergent branches of the tibial apophysis (Fig. 2e) together with a prolateral keel wide and entire on male palpal bulb (Fig. 2a). Female differs from the other species by the shape of the spermathecae with two seminal reeeptacles bifurcated. Female spermathecae resembles *E. antai* (Perafán & Pérez-Miles, fig. 3a) but differs by the less developed internal receptacle and by the oval chambers (Fig. 3e). This species is

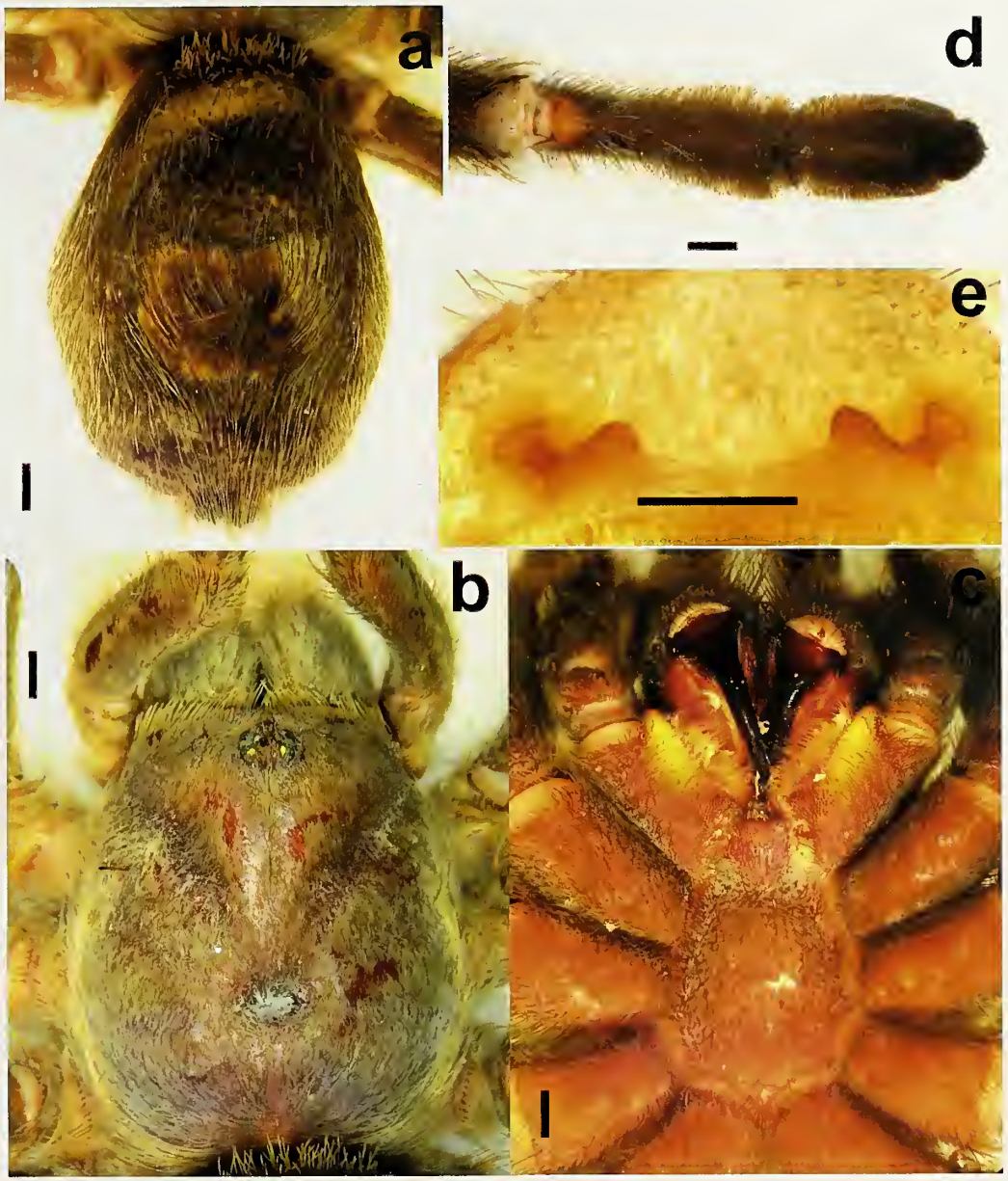

Figure 3.—*Euathlus diamante* sp. nov. female paratype (CAI 3317). a. Abdomen, dorsal view; b. carapace, dorsal view; c. sternum, ventral view; d. tarsus I, ventral view; e. spermathecae, dorsal view. Scale bar = 1 mm.

characterized as inhabiting the Argentinean extra-Andean System with its reproductive period occurring in summer.

Description.—Male holotype (CAI 3330). Color (in alcohol): Cephalothorax and legs light brown (Fig. 2c, d). Abdomen lost. Carapace length 11.1, width 10.2. Anterior eye row slightly procurved, posterior highly recurved. Eyes sizes and interdistances: AME 0.18, ALE 0.14, PME 0.09, PLE 0.15, AME–AME 0.26, AME–ALE 0.10, PME–PME 0.53, PME–PLE 0.05, ALE–PLE 0.11, OQ length 0.9, width 1.2, clypeus 0.4. Fovea transverse, straight, width 1.4. Labium length 0.9, width 1.6 with 102 cuspules. Maxillae (right/left) with 129/134 cuspules. Sternum length 4.5, width 2.7 (Fig. 2d). Chelicerae with six well-developed teeth on promargin of furrow. Tarsi I–IV densely scopulate and entire. Metatarsi I 1/3 scopulate, II 1/2 scopulate, III 1/3, IV 1/4 apically scopulate. Leg and palpal segments lengths in Table 2. Spination: Femora of palp and legs I and IV, 0; II 1-1-1 P, 1 R; III 1-1 R, 1 P. Patellae: palp 1 P; I 1 V, 1-1 R; II, III and IV, 0. Tibiae: palp 2-2 V, 1-1 R; I 2-2 V, 2-1 R, 1-1-1 P; II 2-2-2 V, 1-1-1 R; III 2-2-2 V, 2-1-1-2 P, 2-2-1-2 R; IV 2-1-2-2 V, 1-1-2-2 P, 1-1-1-1-2 R. Metatarsi: I 1 V; II 1-1-1 V; III 2-2-2 V, 1-1-2 R, 2-2-2 P; IV 1-2-2 V, 1-1-1 P, 1-1-1 R. Tarsi I–IV, 0. Metatarsus I straight. Tibia I with retrolateral branch noticeably longer than prolateral; PB with a basal internal short spine, RB with an external and one internal subapical spine (Fig. 2e). Flexion of metatarsus I on the RB. Palpal organ with unequal prolateral keels, well-developed PS, and wide PI with small teeth on the curvature of the embolus (Fig. 2a, b).

Female paratype (CAI 3317). Color (in alcohol): Carapace and legs brownish with patellar lines evident, abdomen brown (Fig. 3a, b). Brown setae on body mixed with golden setae. Total length, not including chelicerae, nor spinnerets, 34.

Table 2.—*Euathlus diamante* sp. nov., length of leg and palpal segments of male.

	I	II	III	IV	Palp
Femur	9.9	9.6	10.2	9.0	6.0
Patella	5.4	5.0	5.1	4.7	4.1
Tibia	8.0	7.7	7.5	7.1	5.1
Metatarsus	7.8	7.2	6.5	8.0	–
Tarsus	5.8	6.2	5.3	6.1	2.2
Total	36.9	35.7	34.6	34.9	17.4

Carapace length, 15.5, width 13.4. Anterior eye row procurved, posterior recurved. Eyes sizes and interdistances: AME 0.21, ALE 0.26, PME 0.20, PLE 0.21, AME–AME 0.46, AME–ALE 0.22, PME–PME 0.77, PME–PLE 0.10, ALE–PLE 0.20, OQ length 1.2, width 1.7, clypeus 0.7. Fovea transverse, straight, width 2.1. Labium length 2.1, width 1.9 with 147 cuspules. Maxillae (right/left) with 142/139 cuspules. Sternum length 6.8, width 4.6 (Fig. 3c). Chelicerae with eight well-developed teeth on promargin of furrow and five small teeth on the proximal area of furrow. Tarsi I–IV densely scopulate and entire (Fig. 3d). Metatarsi I fully scopulate, II 1/2 scopulate, III 1/3, IV 1/4 apically scopulate. Leg and palpal segments lengths in Table 3. Spination: Femora I–IV, patellae of palp and legs I–IV and tarsi I–IV 0. Tibiae: palp 1-2 V, 1-2 P; I 1-3 V, 1 P; II 1-2 V, 1-1 P; III 1-2 V, 1-1 P, 2-2-1 R; IV 1-2 V, 1-1-1 P, 1-1-1 R. Metatarsi: I 1-1 V; II 1-1 V; III 1-1-2 V, 1-1-1 R, 1-2-1 P; IV 1-2 V, 1-1-1 R, 1-1-1 P. Type III and IV urticating setae present. PMS well-developed, PLS normal, apical segment digitiform. Spermathecae with two bifurcated seminal receptacles with lateral oval chamber (Fig. 3e).

Distribution and natural history.—Known from central western Mendoza province, Argentina, at the Andean foothills (Fig. 10). *Euathlus diamante* sp. nov. was found in the Diamante Volcano. The habitat is a high altitude grassland (elevation of about 2200 m), charcterized mainly by *Poa ligularis* Nees ex Steud. (Poaceae) and *Stipa speciosa* Trin. & Rupr. (Poaceae) (Roig et al. 1998). This volcano is located the middle of the Patagonia biogeographical province, on shrubland steppes on sandy floors, with *Neosparton aphyllum* (Gillies & Hook.) Kuntze (1898) (Verbenaceae) alternating with dune vegetation dominated by *Sporobolus rigens* E. Desv. (Poaceae). The mean annual temperatures are about 10 C, and mean annual precipitation of 300 mm (Páez et al. 2004). The adult male sampled was caught using pitfall traps (presumably walking) during January (summer in southern hemisphere) and the female, also captured with pitfall trap was active during the same season (February), thus *E. diamante* sp. nov. is most likely a summer breeding species.

Table 3.—*Euathlus diamante* sp. nov., length of leg and palpal segments of female.

	I	II	III	IV	Palp
Femur	10.7	9.8	9.2	11.5	7.3
Patella	7.0	6.0	5.0	5.5	4.4
Tibia	7.9	6.7	6.5	7.2	6.0
Metatarsus	6.3	6.9	6.7	9.7	–
Tarsus	4.4	4.5	4.3	5.7	4.6
Total	36.3	33.9	31.7	39.6	22.3

Table 4.—*Euathlus sagei* sp. nov., length of leg and palpal segments of male.

	I	II	III	IV	Palp
Femur	10.1	9.9	9.0	11.0	6.2
Patella	5.3	5.6	5.4	6.1	4.2
Tibia	7.4	7.8	7.0	7.9	5.8
Metatarsus	7.3	7.4	8.3	9.4	–
Tarsus	5.3	5.2	4.9	5.5	2.8
Total	35.4	35.9	34.6	39.9	19.0

Euathlus sagei new species
Figs. 4–6, Tables 4 & 5

Type material.—Male holotype: ARGENTINA: *Neuquén*: Zapala department, Parque Nacional Laguna Blanca, approximately 300 meters southwest of Atiñir lake, elevation 1360 m, 27 February 2009, R. Sage (MACN-Ar 32685). Female paratype: ARGENTINA: *Neuquén*: near Zapala city (39.0233° S, 70.0208° W), elevation 979 m, 30 October 2011, N. Ferretti (MACN-Ar 32686).

Additional material examined.—ARGENTINA: *Neuquén*: Zapala department, near Zapala city (39.0561° S, 70.3469° W), elevation 1185 m, 30 October 2011, N. Ferretti (LZI 344), 1 juvenile; Zapala department, near Zapala city (39.0782° S, 70.5466° W), elevation 1345 m, 30 October 2011, N. Ferretti (LZI 345), 1 juvenile.

Etymology.—This species is a patronym, named in honor of the naturalist Richard D. Sage from the Sociedad Naturalista Andino Patagónica (SNAP), who has collected and kindly donated a specimen belonging to this new species.

Diagnosis.—Male differs from the other *Euathlus* species by the PI evidently truncated in the embolus (Fig. 4a) in combination with a serrated tip (Fig. 4b). Female differs from other *Euathlus* species by the shape of the spermathecae with long basis and parallel to epigastric furrow (Fig. 5e) and scopulae divided on tarsi III and IV (Fig. 5d). This species is characterized as inhabiting the patagonic steepe with the reproductive period occurring in summer.

Description.—Male holotype (MACN-Ar 32685). Color (in alcohol): Cephalothorax reddish brown with light grey small setae and golden long setae on margins; abdomen with long brown setae and a patch of red setae on the anterior-dorsal face; sternum, coxa and trochanter reddish (Fig. 4c, e). Total length, not including chelicerae, nor spinnerets, 26.2. Carapace

Table 5.—*Euathlus sagei* sp. nov., length of leg and palpal segments of female.

	I	II	III	IV	Palp
Femur	6.5	6.0	5.9	6.0	5.2
Patella	2.5	3.1	2.5	3.7	2.7
Tibia	5.1	4.0	4.1	5.1	3.7
Metatarsus	3.1	3.0	3.4	4.8	–
Tarsus	2.5	2.9	3.0	3.7	3.1
Total	19.7	19.0	18.9	22.6	14.7

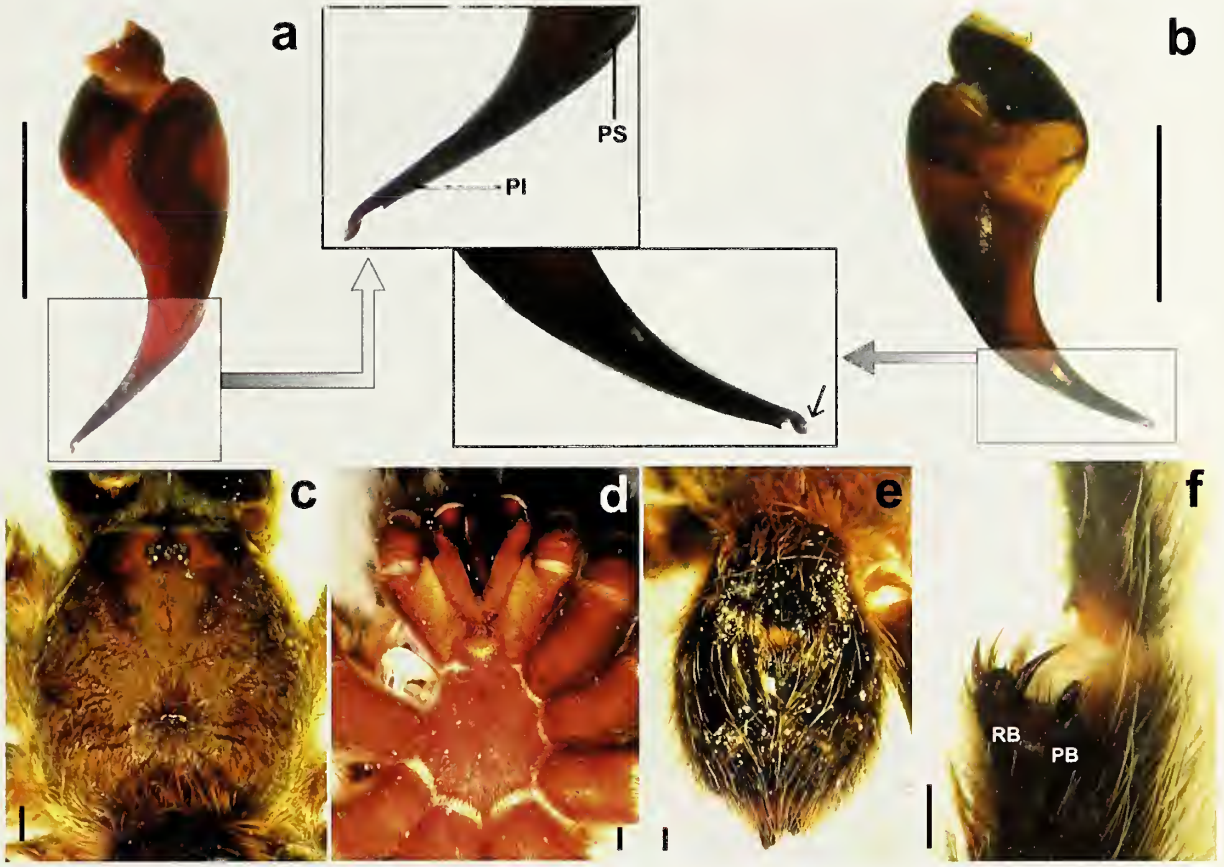

Figure 4.—*Euathlus sagei* sp. nov. male holotype (MACN-Ar 32685). a. Palpal organ, prolateral view, the box indicates the apical embolus with keels; b. palpal organ, retrolateral view, the arrow inside the box indicates the serrated apical embolus; c. carapace, dorsal view; d. sternum, ventral view; e. abdomen, dorsal view; f. tibial apophysis, ventral view. PS = prolateral superior keel, PI = prolateral inferior keel, PB = prolateral branch, RB = retrolateral branch. Scale bar = 1 mm.

length 12.6, width 11.5. Anterior eye row procurved, posterior recurved. Eyes sizes and interdistances: AME 0.19, ALE 0.20, PME 0.18, PLE 0.21, AME–AME 0.45, AME–ALE 0.27, PME–PME 0.75, PME–PLE 0.11, ALE–PLE 0.19, OQ length 1.2, width 1.6, clypeus 0.3. Fovea transverse, slightly recurved, width 1.2. Labium length 1.2, width 1.4 with 79 cuspules. Maxillae (right/left) with 121/125 cuspules. Sternum length 5.8, width 4.5 (Fig. 4d). Chelicerae with six well-developed teeth on promargin of furrow and five small teeth on retromargin. Tarsi I–IV densely scopulate and entire. Metatarsi I fully scopulate, II 2/3 scopulate, III 1/2, IV 1/4 apically scopulate. Leg and palpal segments lengths in Table 4. Spination: Femora of palp and legs I–IV, 0. Patellae: palp 1 P; I 1 V, 1 R; II 1-1 P; III and IV, 0. Tibiae: palp 1-2-1 P, 1-1 V; I 1-1-2-1-1-2 V, 1-1 R, 1-1 P; II 2-1-2-1-2 V, 1-1-1 R, 2-1-1-1 P; III 1-1-2 V, 1-1-1 P, 1-1 R; IV 1-1-2 V, 1 P, 1-1-1 R. Metatarsi: I 1 V; II 1-1 V; III 1-1-1 V, 1-1-1 R, 1-1 P; IV 2-1-1-1-2 V, 1-1 P, 1-1-1-2 R. Tarsi I–IV, 0. Metatarsus I slightly curved. Tibia I with retrolateral branch longer than prolateral; PB with an apical strong spine, RB with an internal and external subapical strong and long spines (Fig. 4f). Flexion of metatarsus I retrolateral to the tibial apophysis. Type III urticating setae present. PMS well-developed, PLS normal, apical segment digitiform. Palpal organ with flat and subequal less developed prolateral keels and serrated tip of embolus; flat PS long and closer to PI, and PI evidently truncated in the apical third of the embolus (Fig. 4a, b).

Female paratype (MACN-Ar 32686). Color (alive specimem): Cephalothorax reddish brown with light grey small setae and golden long setae on margins; abdomen with long brown setae and a patch of red setae on anterior-dorsal face; sternum, coxa and trochanter reddish with orange setae around spinnerets (Figs. 5a, b; 6a–c). Total length, not including chelicerae, nor spinnerets, 21.6. Carapace length, 8.1, width 7.0. Anterior eye row procurved, posterior recurved. Eyes sizes and interdistances: AME 0.17, ALE 0.16, PME 0.12, PLE 0.12, AME–AME 0.34, AME–ALE 0.09, PME–PME 0.63, PME–PLE 0.06, ALE–PLE 0.10, OQ length 0.9, width 1.3, clypeus 0.2. Fovea transverse, straight, width 0.8. Labium length 1.2, width 1.1 with 47 cuspules. Maxillae (right/left) with 108/111cuspules. Sternum length 3.4, width 2.8 (Fig. 5c). Chelicerae with seven well-developed teeth on promargin of furrow and eight small teeth on the proximal area of furrow. Tarsi I–II densely scopulate and entire, tarsus III fully scopulate divided by a paired setal row and IV fully scopulate divided by a four setal row (Fig. 5d). Metatarsi I and II 1/2 scopulate and entire, III 1/3 and divided by a row of single seta, IV 1/4 apically scopulate and divided by a row of paired setae. Leg and palpal segments lengths in Table 5. Spination: Femora III–IV, patellae of palp and legs I–IV and tarsi I–IV 0. Femur: palp 1 D; I 1 P; II 1 P. Tibiae: palp 1-1-2 V, 1-1 P, 1 R;

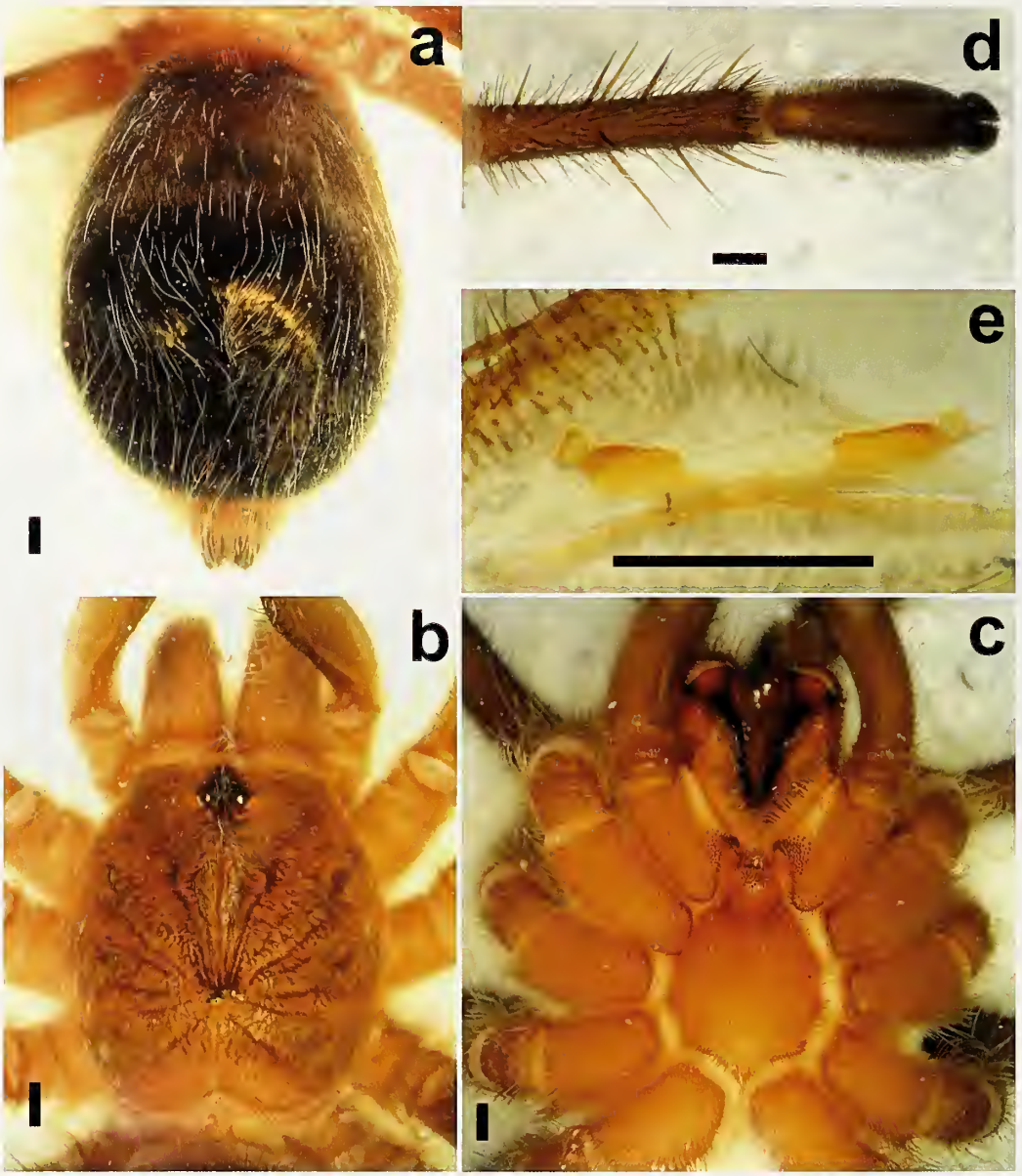

Figure 5.—*Euathlus sagei* sp. nov. female paratype (MACN-Ar 32686). a. Abdomen, dorsal view; b. carapace, dorsal view; c. sternum, ventral view; d. tarsus IV, ventral view; e. spermathecae, dorsal view. Scale bar = 1 mm.

I 1 V; II 1-1 V; III 1-1-2 V, 1-2-1 P; IV 1-1-2 V, 1 P. Metatarsi: I 1-1 V; II 1-1 V; III 2-2-2 V, 1-1 P, 1-1-1 R; IV 2-2-1-2 V, 1-1 P, 1-2-1 R. Type III and IV urticating setae present. PMS well-developed, PLS normal, apical segment digitiform. Spermathecae with two wide and right-angled seminal receptacles each with a lateral rounded chamber pointing laterally (Fig. 5e).

Distribution and natural history.—Known from central Neuquén province, Argentina (Fig. 10). *Euathlus sagei* sp. nov. inhabits small crevices and short burrows under stones at the patagonic steppe. The habitat where this species was located comprises hilly areas of about 1100 and 1400 meters above sea level (m.a.s.l) and shrubby plateau (Fig. 6d). Some of the characteristic vegetation was *Jarava speciosa* (Trin. & Rupr.) (Poaceae), *Nassauvia glomerulosa* (Lag. ex Lindl.) D. Don (Asteraceae), *Mulinum spinosum* (Cav.) Pers. (Apiaceae), *Senecio bracteolatus* Hook & Arn. (Asteraceae), *Bromus tectorum* L. (Poaceae) and *Poa lanuginosa* (Poir.) (Poaceae) (Villamil & Testoni 2012). The mean minimum temperature is 1.7°C (July) and the mean maximum is 16°C (January) with a mean annual temperature of approximately 9°C. The mean annual precipitation is about 200–250 mm. Winds are of high frequencies and speed (150 km/h) through the year, predominately from the west (Gandullo et al. 2011). The adult male was captured walking during February (summer in southern hemisphere), thus the reproductive period seems to occur at this time.

Euathlus tenebrarum new species
Figs. 7–9, Tables 6 & 7

Type material.—Male holotype: ARGENTINA: *Neuquén*: Huiliches department, next to Curruhué Chico lake (39.9078 S, 71.3328 W), elevation 1042 m, 28 October 2011, L. Schwerdt

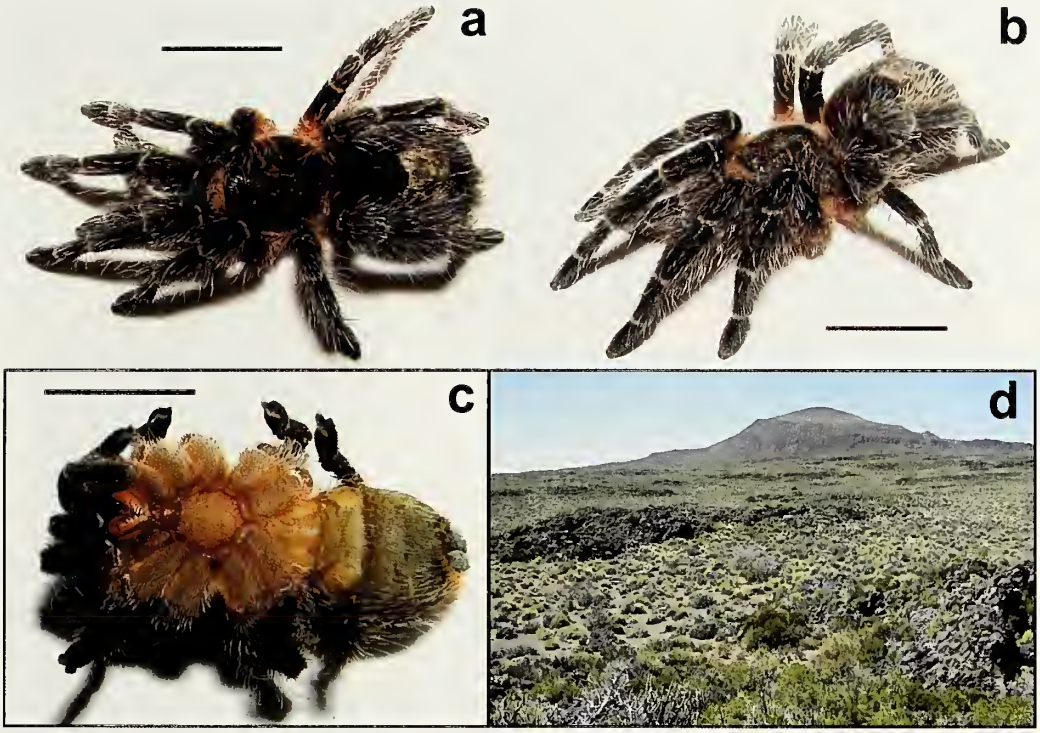

Figure 6.—*Euathlus sagei* sp. nov. female paratype (MACN-Ar 32686). a. a—c. Habitus; d. image depicting the habitat at the type locality. Scale bar = 1 cm.

(MACN-Ar 32687). Female paratype: ARGENTINA: *Neuquén:* Ñorquin department, Copahue (37.7964 S, 71.1167 W), 25 March 2009, R. Sage (MACN-Ar 32688).

Etymology.—The specific name is "dark place" in *Latin*. Moreover, dark place corresponds to the meaning of "Curruhué" in Mapuche language, a dialect isolate spoken in south-central Chile and west-central Argentina by the Mapuche people. "Curruhué" is a name of a lake near to where this species was found.

Diagnosis.—Male differs from the other *Euathlus* species by a tibial apophysis with branches almost of equal sizes (Fig. 7e) and by an abruptly tapered bulb shape (Fig. 7a, b). Female differs from other *Euathlus* species by the shape of the spermathecae with two wide seminal receptacles with a lateral spheroid chamber not oriented apicolateral in opposition to the epigastric furrow (Fig. 8e). This species is characterized as inhabiting the Andean patagonic-forests with its reproductive period occurring in spring.

Description.—Male holotype (MACN-Ar 32687). Color (in alcohol): Cephalothorax with light grey small setae and golden long setae on margins and dorsal chelicerae; abdomen with a large patch of red setae on the anterior-dorsal face (Figs. 7c, d; 9a). Total length, not including chelicerae, nor spinnerets, 20.1. Carapace length 9.7, width 8.2. Anterior eye row procurved, posterior recurved. Eyes sizes and interdistances: AME 0.21, ALE 0.25, PME 0.14, PLE 0.21, AME–AME 0.28, AME–ALE 0.09, PME–PME 0.57, PME–PLE 0.08, ALE–PLE 0.13, OQ length 0.8, width 1.2, clypeus 0.2. Fovea transverse, slightly recurved, width 1.8. Labium length 0.6, width 0.8 with 96 cuspules. Maxillae (right/left) with 118/120 cuspules. Sternum length 4.8, width 3.2 (Fig. 7d). Chelicerae with nine well-developed teeth on promargin of furrow and seven small teeth on retromargin. Tarsi I–IV densely scopulate and entire. Metatarsi I fully scopulate, II 1/2 scopulate, III 1/2, IV 1/3 apically scopulate. Leg and palpal segments lengths in Table 6. Spination: Femur IV and patellae of palp and legs I–IV, 0. Femora: palp 1 P; I 1 D; II 1 P; III 1 P. Tibiae: palp 1-1-2-1 P, 1 V; I 2-1-2-1 V, 1-1 R, 2-1-2-1 P; II 1-1-2-1-2 V, 1 R, 2-1-1-1 P; III 1-1 V, 1-1-2-1 P, 1-1 R; IV 1-1-2 V, 1-2-1 P, 1-2-2 R. Metatarsi: I 0; II 2 V; III 1-2-2 V, 1-1 R, 1-2-1-1 P; IV 2-1-1-2 V, 1-1-1-1 P, 1-1-1 R. Tarsi I–IV, 0. Metatarsus I slightly

Table 6.—*Euathlus tenebrarum* sp. nov., length of leg and palpal segments of male.

	I	II	III	IV	Palp
Femur	8.4	7.3	7.2	7.7	4.4
Patella	4.1	4.2	3.5	4.4	3.2
Tibia	6.5	5.8	5.5	6.3	4.3
Metatarsus	6.1	6.6	6.4	7.6	–
Tarsus	4.1	4.2	4.3	5.2	2.2
Total	29.2	28.1	26.9	31.2	14.1

Table 7.—*Euathlus tenebrarum* sp. nov., length of leg and palpal segments of female.

	I	II	III	IV	Palp
Femur	7.3	6.8	5.4	7.7	5.6
Patella	4.4	4.3	3.5	4.4	3.0
Tibia	5.5	5.4	5.1	5.4	4.1
Metatarsus	4.3	4.2	5.0	7.5	–
Tarsus	2.9	3.6	3.5	4.3	3.3
Total	24.4	24.3	22.5	29.3	16.0

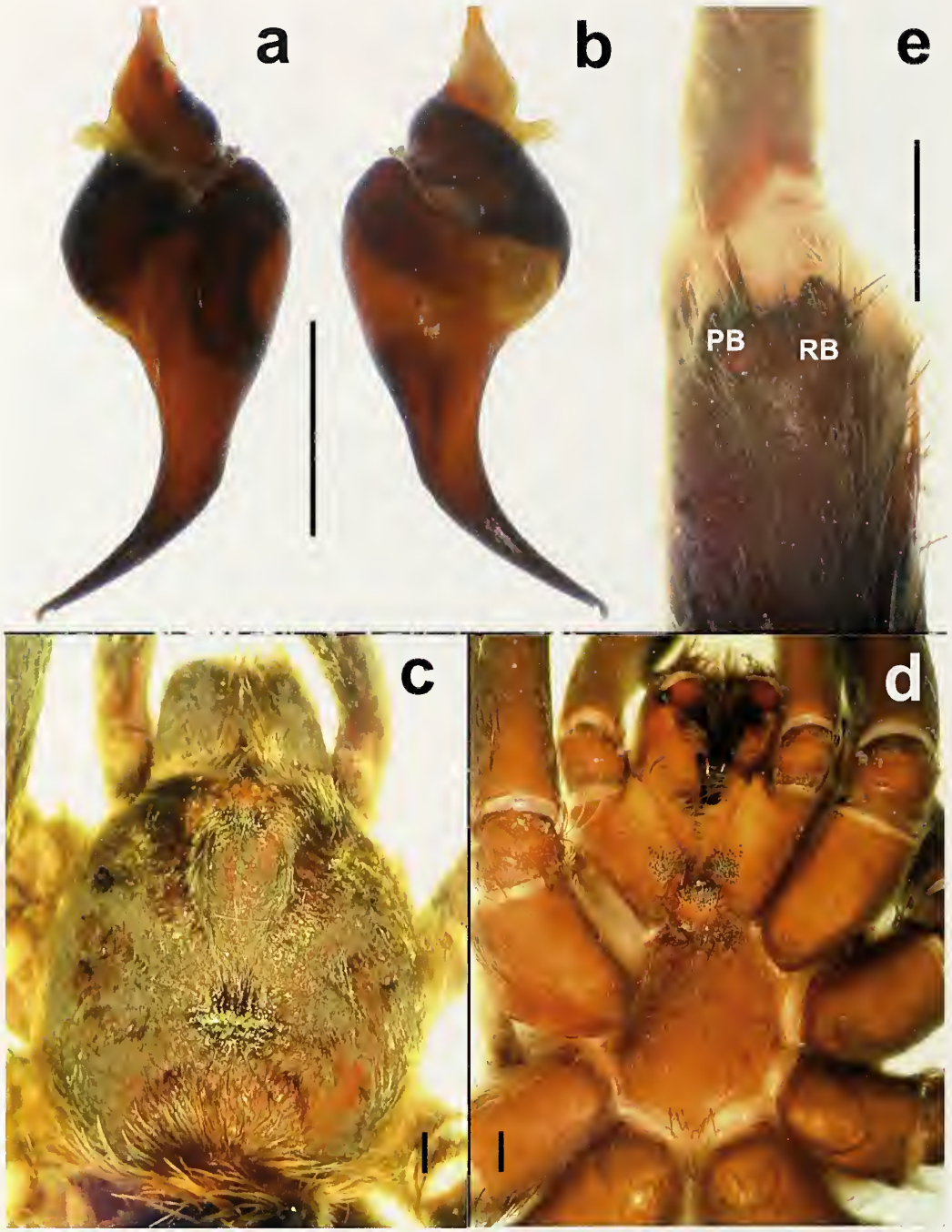

Figure 7.—*Euathlus tenebrarum* sp. nov. male holotype (MACN-Ar 32687). a. Palpal organ, prolateral view; b. palpal organ, retrolateral view; c. carapace, dorsal view; d. sternum, ventral view; e. tibial apophysis, ventral view. PB = prolateral branch, RB = retrolateral branch. Scale bar = 1 mm.

curved. Tibia I possesses short apophyses with retrolateral branch slightly longer than prolateral; PB with an apical strong long spine, RB with an internal subapical short spine (Fig. 7e). Flexion of metatarsus I retrolateral to the tibial apophysis. Type III and IV urticating setae present. PMS well-developed, PLS normal, apical segment digitiform. Palpal organ abruptly tapering with flat and subequal less developed prolateral keels; flat PS long and closer to PI, and PI evidently truncated in the apical third of the embolus (Fig. 7a, b).

Female paratype (MACN-Ar 32688). Color (in alcohol): Carapace and legs brownish with patellar lines evident, abdomen brown (Fig. 8a, b). Brown setae on body mixed with golden setae. Total length, not including chelicerae, nor spinnerets, 23.6. Carapace length, 10.1, width 9.8. Anterior eye row procurved, posterior recurved. Eyes sizes and interdistances: AME 0.14, ALE 0.11, PME 0.16, PLE 0.12, AME–AME 0.29, AME–ALE 0.17, PME–PME 0.55, PME–PLE 0.06, ALE–PLE 0.23, OQ length 0.9, width 1.2, clypeus 0.3. Fovea transverse, slightly recurved, width 1.1. Labium length 1.2, width 1.4 with 68 cuspules. Maxillae (right/left) with 132/137 cuspules. Sternum length 4.6, width 3.9 (Fig. 8c). Chelicerae with seven well-developed teeth on promargin of furrow and six small teeth on the proximal area of furrow.

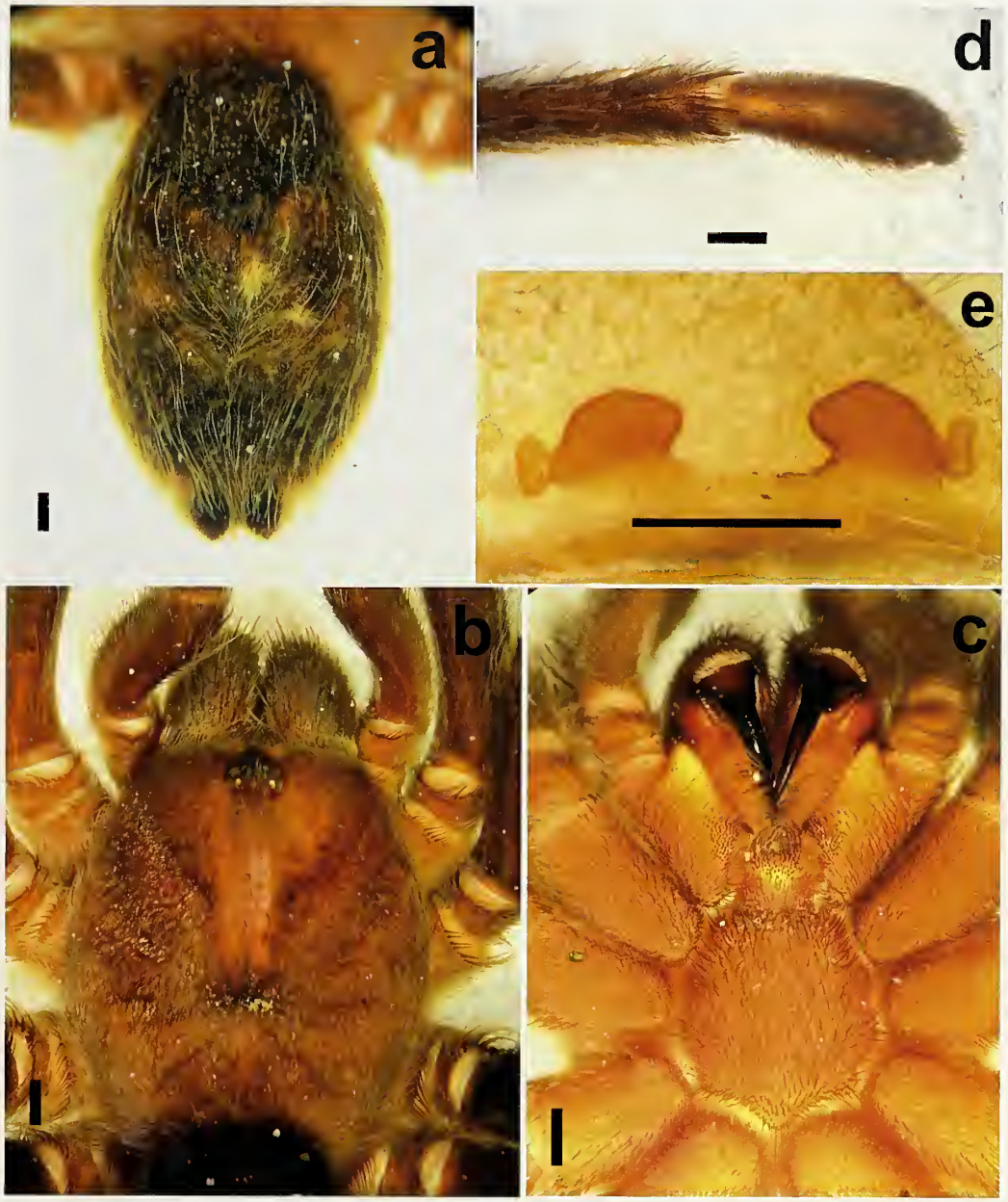

Figure 8.—*Euathlus tenebrarum* sp. nov. male holotype (MACN-Ar 32687). a. Abdomen, dorsal view; b. carapace, dorsal view; c. sternum, ventral view; d. tarsus IV, ventral view; e. spermathecae, dorsal view. Scale bar = 1 mm.

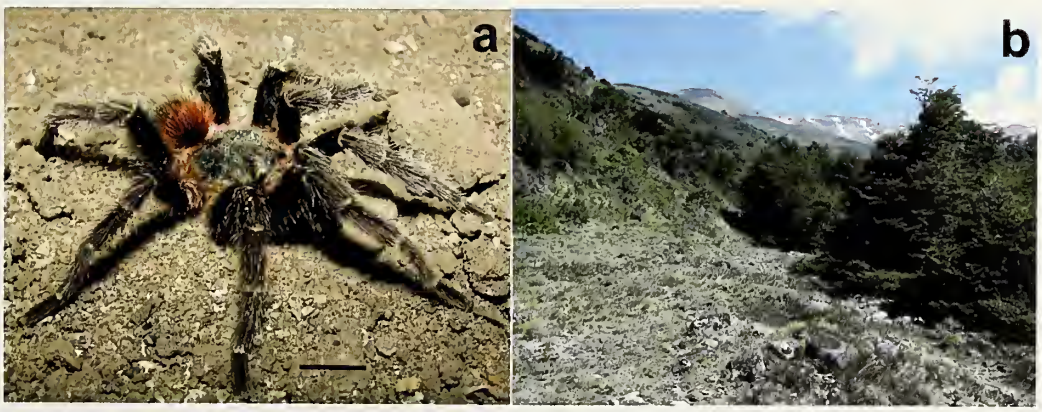

Figure 9.—*Euathlus tenebrarum* sp. nov. male holotype (MACN-Ar 32687). a. In life; b. image depicting the habitat at the type locality. Scale bar = 1 cm

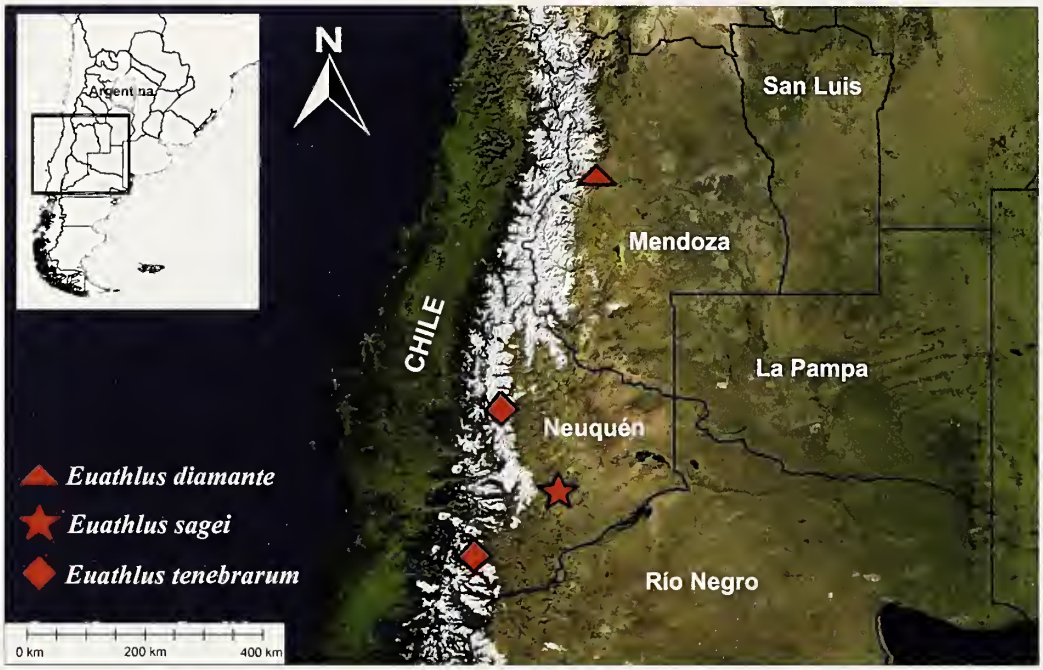

Figure 10.—Map showing the distribution of the *Euathlus* species treated in this work.

Tarsi I–III densely scopulate and entire, tarsus IV fully scopulate divided by a three-setal row. Metatarsi I fully scopulate divided by a row of single setae, II 1/2 scopulate and divided by a row of single setae, III 1/3 and divided by a row of paired setae, IV 1/4 apically scopulate and divided by a row of four setae (Fig. 8d). Leg and palpal segments lengths in Table 7. Spination: Femora I–III, patellae of palp and legs I–IV and tarsi I–IV 0. Femur: IV 1 R. Tibiae: palp 1-1-2 V, 1-1-1 P, 1 R; I 1-2 V, 1 P; II 2 V, 1-1 P; III 1-2 V, 1-1-1-2 P, 1 R; IV 1-2 V, 1-1-1 P, 1-1-1 R. Metatarsi: I 1-1 V; II 1-1 V; III 1-1-1 V, 1-2-2 P, 1-2 R; IV 2-2-2 V, 1-1 P, 1-1-1-2 R. Type III and IV urticating setae present. PMS well-developed, PLS normal, apical segment digitiform. Spermathecae with two wide seminal receptacles with spheroid chamber pointing laterally (Fig. 8e).

Distribution and natural history.—Known from western Neuquén province, Argentina, at the Andean-patagonic forests (Fig. 10). The male holotype was found in October (spring in southern hemisphere) under a stone with no evident burrow or shelter, thus it was most likely wandering during this period. In this region the mean minimum temperature is −2 °C (July), the mean maximum is 23 °C (January), and the mean annual temperature is 8 °C. Precipitation is concentrated mainly in autumn and winter, and it occurs as snow, with an annual rainfall of 1700 mm (Barros et al. 1983). At this latitude, mean precipitation decreases abruptly from about 4000 mm/year on the western side of the Andes to less than 500 mm/year, only 80 km to the east (De Fina 1972). In the wetter area, the lowland rain forests are mainly dominated by the evergreen *Nothofagus dombeyi* (Mirb.) Oerst. (Nothofagaceae). In the intermediate parts of the precipitation gradient, at low elevations, *N. dombeyi* forms monospecific mesic forests or mixed stands of the conifer *Austrocedrus chilensis* (D. Don) Pic. Serm. & Bizzarri (Cupressaceae) at drier sites; in the eastern region, conifers shift to relatively open woodlands (Fig. 9b). In the western and central areas, forest understory is typically dominated by dense and tall (> 2 m) populations of *Chusquea culeou* Desvaux (Poaceae) (Mermoz et al. 2005).

DISCUSSION

Euathlus was recently revised (Perafán & Pérez-Miles 2014) and most species are recorded for Chile, with *E. truculentus* only recorded for Argentina in the province of Catamarca (north western Argentina) (Schiapelli & Gerschman 1963). The descriptions of these three new species represent southern records for the genus in Argentina inhabiting very distinct habitats. The most geographically proximal species are *E. truculentus* and *E. diamante* sp. nov., the latter located more than 700 km south relative to *E. truculentus*. The other two new species are described from Neuquén province but inhabit different habitats. *E. tenebrarum* sp. nov. is located at high altitudes in Andean patagonic forests and *E. sagei* sp. nov. lives east of the Andean hills, in the extreme aridity of the patagonic steppe.

It is known that the Theraphosidae is a group that presents enormous morphological homogeneity and many taxonomic problems (Raven 1990; Bertani 2000) and many of the descriptions involve structures such as stridulatory organs, fovea shape, small differences in the proportions between leg articles and other body parts, size and disposition of the eyes and scopulae, and color patterns (Schiapelli & Gerschman de Pikelin 1979; Raven 1985; Smith 1995; Prentice 1997). Many of these characters are conservative, but some new species were described based either on plesiomorphies or slight morphological variations (Bertani 2000). Although descriptions of these new species in the present work only refer to a single couple of specimens (holotype male and paratype

female), the classification and identification is based mainly on genital structures, such as shape of spermathecae and palpal bulb features (mainly keels). These characters are conservative and in recent years have been shown in the Theraphosidae to be constant and useful in characterizing the taxa (Pérez-Miles et al. 1996; Bertani 2000, 2001; Perafán & Pérez-Miles 2014). Moreover, as recently proposed by Ortiz & Francke (2015), the male pedipalpal bulbs' structures are fundamental in Theraphosinae spiders' taxonomy as they are very often used as the cornerstone to differentiate between genera and species in the group. Also, other taxonomic characters sueh as extent of metatarsal scopulation and condition of tarsal scopula (entire or divided) were used and have been proven to have high discriminating value (Prentice 1997).

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Description of the first visually cryptic species of *Paratropis* (Araneae: Paratropididae) from Ecuador

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Abstract. A new species of Paratropididae is described, *Paratropis elicioi* n. sp., representing the first record of the family Paratropididae from Ecuador. A key to the genera of the subfamily Paratropidinae is provided.

Keywords: Spider, Mygalomorphae, taxonomy, new species

In May 2014, the spider biodiversity project of the cloud forest in the Chocó region of Ecuador was launched; its goal, to uncover the spider diversity hidden among the clouds. I present here our first discovery, the occurrence of the family Paratropididae in Ecuador with the description of a new species *Paratropis elicioi* n. sp. The family Paratropididae is composed of 10 species distributed in four genera, occurring in Mexico, Central America and South America (World Spider Catalogue 2014). Paratropididae are visually cryptic (camouflaged) spiders that live hidden in the dirt and can be recognized by their elevated eye tubercle, their weakly or ascopulate tarsi and a body encrusted with soil and dirt (Raven 1985:121).

The family includes two subfamilies, Paratropidinae and Glabropelmatinae (Raven 1985:121). The subfamily Paratropidinae is recognized by the presence of a long single tooth on tarsal claws, the steeply elevated eye tubercle and the absence of both a tibial spur and claw tufts (Raven 1985:121). Paratropidinae is composed of three genera: *Paratropis* Simon 1889, *Anisaspis* Simon 1891, *Anisaspoides* F.O.P-Cambridge 1896 (Raven 1985:121). The genus *Paratropis* Simon 1889 includes five species from which only two males have been described, *P. papilligera* F.O.P.-Cambridge 1896 and *P. tuxtelusis* Valdez-Mondragón, Mendoza & Francke 2014.

The genus *Paratropis* was originally differentiated from other Paratropidinae genera by the presence of a third claw on leg I and the absence of the third claw on leg II (Raven 1985:122). Valdez-Mondragón et al. (2014) mentioned that the female of their new species had a small, third claw on leg II. The new species presented here lacks the third claw on all legs. For now, the presence or absence of a third claw on legs I–II is an ambiguous character and cannot be used to define the species that are currently placed in the genus *Paratropis*. As mentioned by Valdez-Mondragón et al. (2014), further work is needed to test the validity of *Paratropis* and the other Paratropidinae genera. Valdez-Mondragón et al. (2014) diagnosed the genus using the combination of eight characters; unfortunately most of these characters pertain to the subfamily Paratropidinae, and are not helpful in recognizing the genus *Paratropis*. A simple key based on the information given by Raven (1985) is proposed in order to help distinguish between the different Paratropidinae genera.

KEY TO THE GENERA OF THE SUBFAMILY PARATROPIDINAE

1. Four spinnerets ..... *Paratropis*
   Two spinnerets 2
2. Teeth on both margins in two diagonally opposed rows ..... *Anisaspis*
   Teeth on both margins in two juxtaposed rows ..... *Anisaspoides*

METHODS

Specimens were examined in 70% ethanol under a SMZ-U Nikon dissection microscope. A Nikon Coolpix 950 digital camera attached to the microscope was used to photograph all the structures to be illustrated. The digital photos were used to trace proportions and the illustrations were detailed and shaded by referring back to the structure under the microscope. Female genitalia were excised using a sharp entomological needle, washed in 80% alcohol, placed on a slide in lactic acid and observed under an AmScope XSG Series T-500 compound microscope. The structure was photographed and illustrated as explained above. Tarsal claws were observed and photographed under an AmScope XSG Series T-500 compound microscope. All measurements are in millimeters and were made using a micrometric ruler fitted on the eyepiece of the microscope.

ABBREVIATIONS

Somatic.—AME: anterior median eye; ALE: anterior lateral eye; PME: posterior median eye; PLE: posterior lateral eye; PLS: posterior lateral spinnerets; PMS: posterior median spinnerets.

Genitalia.—***Female*:** s: spermathecae; ve: vesicles; ***Male*:** b: bulb; e: embolus.

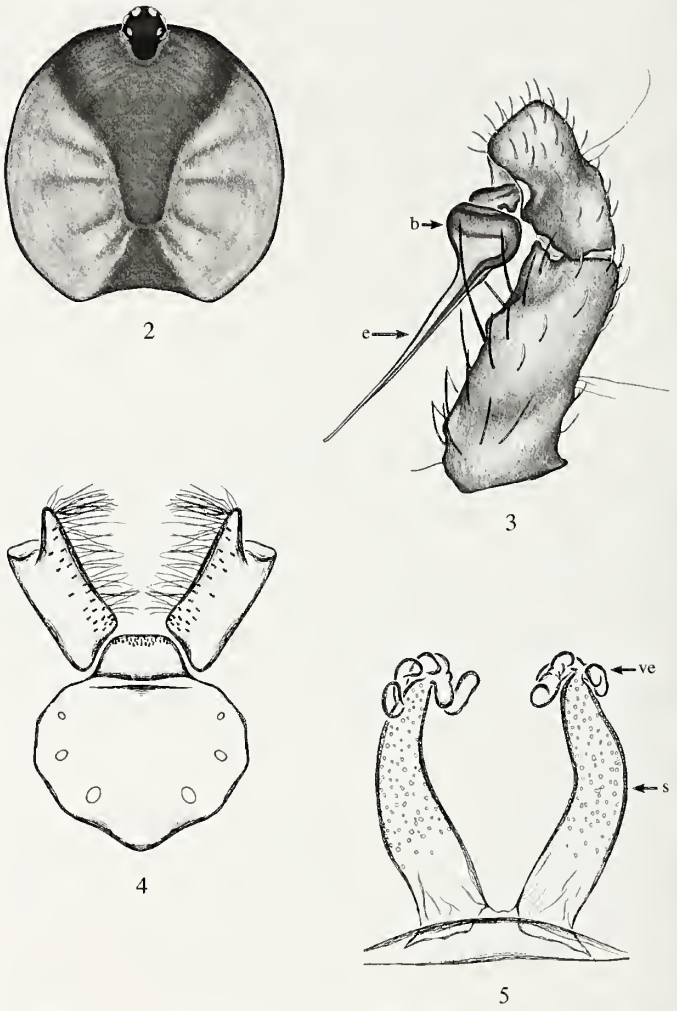
TAXONOMY

Paratropis Simon 1889

Type species.—*Paratropis scruposa* Simon 1889.

Composition.—*P. elicioi* **n. sp.**, *P. papilligera* F.O.P.-Cambridge 1896, *P. sanguinea* Mello-Leitão 1923, *P. scruposa* Simon 1889, *P. seminermis* Caporiacco 1955, *P. tuxtelnsis* Valdez-Mondragón, Mendoza & Francke 2014.

Figure 1.—Male holotype of *Paratropis elicioi* new species.



Figures 2–5.—*Paratropis elicioi* new species. Male 2–4. Female 5. 2. Carapace, dorsal view. 3. Palp, retrolateral view. 4. Sternum and endites, ventral view. 5. Internal genitalia, dorsal view.

Distribution.—Mexico, Venezuela, Ecuador, Brazil and Peru.

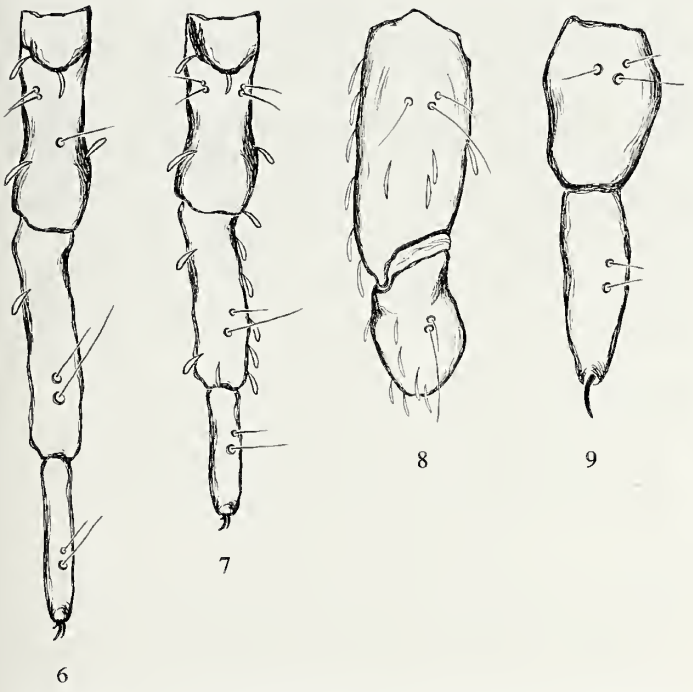
Paratropis elicioi **new species**
Figs. 1–13

Type material.—Male holotype from Ecuador, Cotopaxi Province, Otonga Biological Reserve (00.41941°S, 78.99607°W), 1717 m, pitfall near Rio Esmeraldas, 25.xi–08.xii.2014, N. Dupérré & E. Tapia (QCAZ). Female paratype from Ecuador, Cotopaxi Province, Otonga Biological Reserve (00.41941°S, 78.99607°W), 1717 m, pitfall near Rio Esmeraldas, 03–16.viii.2014, N. Dupérré & E. Tapia (QCAZ).

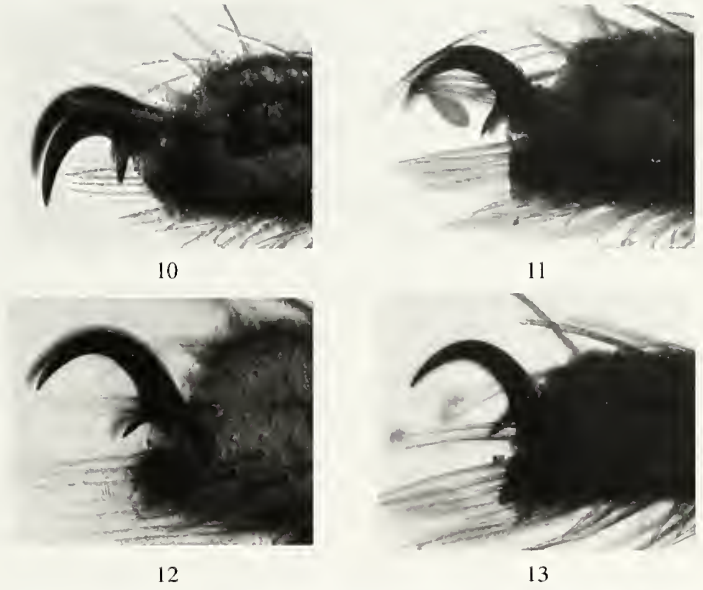
Etymology.—The specific epithet is in honor of biologist, Elicio Eladio Tapia for his work in discovering and preserving Ecuador's biodiversity.

Diagnosis.—Males and females can be distinguished from all other *Paratropis* by the absence of the third tarsal claw on all legs (Figs. 10–13). Furthermore, males and females are diagnosed from *P. tuxtelnsis* by their trichobothrial pattern (Figs. 6–9).

Description.—*Male:* Total length: 8.5; carapace length: 3.5; carapace width: 3.3; abdomen length: 5.0. CEPHALOTHORAX: Carapace encrusted with sand and dirt: light brown, covered with long barbed setae along midline and margin, with clubbed setae at base (Fig. 1). Carapace cleaned: slightly longer than wide, concave posteriorly, dark reddish; pars cephalica elevated, black with prominent eye tubercle with narrow base; pars thoracica flat, black; fovea transverse (Fig. 2). Chelicerae brown encrusted with sand and dirt; promargin and retromargin juxtaposed with rows of nine teeth; fang furrow very narrow without denticles. Labium dark reddish brown, without soil, trapezoidal with ~25 cuspules. Maxillae orange brown, without soil, with conical projection anteriorly and ~25 cuspules. Sternum encrusted with sand and dirt, light brown; cleaned dark reddish brown, slightly wider than long, flat, with three oval sigilla (Fig. 4). EYES: Eight eyes on a high tubercle, AME rounded, separated by half their width; LE oval, touching, ALE the largest; PME oval the smallest, separated by three times their diameter; anterior row recurved, posterior row recurved (Fig. 2). ABDOMEN: Inverse heart-shaped, light brown heavily encrusted with dirt and sand; dorsally with five tubercles each bearing a large clubbed seta, depressed in the middle; laterally with one apical tubercle bearing a large clubbed seta, and numerous clubbed setae (Fig. 1); ventrally covered by numerous clubbed setae. Booklung apertures without dirt and sand, oval, well sclerotized. SPINNERETS: PLS light brown, lightly encrusted with dirt and sand; basal and medial short, apical segment cylindrical; respectively 0.3/0.2/0.6; PMS very small,



Figures 6–9.—*Paratropis elicioi* new species. Male 6–8. Female 9. 6. Tibia, metatarsus and tarsus IV, dorsal view. 7. Tibia, metatarsus and tarsus III, dorsal view. 8. Palpal tibia and cymbium, dorsal view. 9. Palpal tibia and tarsus, dorsal view.



Figures 10–13.—*Paratropis elicioi* new species. Male 10–13. 10. Claw I, lateral view. 11. Claw II, lateral view. 12 Claw III, lateral view. 13 Claw IV, lateral view.

light brown, encrusted with dirt and sand. LEGS: Light brown encrusted with dirt and sand, covered with barbed and clubbed setae; leg I without tibial spur; leg formula 1423; total length: I 11.2 II 8.0 III 7.5 IV 10.2; (Fig. 1). Leg trichobothria: tibia IV with three (Fig. 6), tibia I–III with four (as in Fig. 7); metatarsus and tarsus I–IV with two (as in Figs. 6, 7); palpal tibia with three trichobothria, palpal cymbium with two trichobothria (Fig. 8). Paired tarsal claws with one elongated tooth; third claw absent on all legs (Figs. 10–13). GENITALIA: Palpal tibia covered with soil and dirt; palpal cymbium pointed; bulb pyriform; embolus transparent, long and thin almost reaching the base of the tibia, tip slightly curved (Fig. 3).

Female: Total length: 11.5; carapace length: 5.0; carapace width: 4.5; abdomen length: 6.5. CEPHALOTHORAX: As in male. Chelicerae as in male; promargin with row of 10 teeth juxtaposed to retromagin with row of eight teeth; fang furrow narrow without denticles. Labium, maxillae and sternum as in male. EYES: As in male. ABDOMEN: As in male. SPINNERETS: PLS light brown, lightly encrusted with dirt and sand; basal and medial short, apieal segment cylindrical; respectively 0.5/0.3/0.9; PMS very small, light brown, encrusted with dirt and sand. LEGS: as in male; leg formula 4123; total length: I 12.6 II 10.5 III 9.8 IV 14. Leg trichobothria: as in male; palpal tibia with three trichobothria; palpal tarsus with two trichobothria (Fig. 9). Paired and third tarsal claws as in male; palpal tarsus with one claw, without tooth (Fig. 9). GENITALIA: Internal genitalia with elongated spermathecae curved inwards with oval vesicles apically (Fig. 5).

Other material examined.—*Cotopaxi Province:* Otonga Biological Reserve (00.41941°S 78.99607°W), 1717 m, pitfall near Rio Esmeraldas, 1 male, 25.xi–08.xii.2014, N. Dupérré & E. Tapia (DTC); pitfall near Rio Esmeraldas, 1 juvenile, 16.viii–05.ix.2014, N. Dupérré & E. Tapia (DTC); sifting litter, 3 juveniles, 04–07.ix.2014, N. Dupérré, E. Tapia, C. Tapia (DTC); (00.41994°S 79.00623°W), 1997 m, pitfall, 1 juvenile, 05–19.ix.2014, N. Dupérré & E. Tapia (DTC).

Distribution.—Ecuador, Cotopaxi province.

Natural history.—Specimens were collected in a low evergreen montane forest from 1717 m up to 1997 m. At 1717 m, specimens were collected by pitfall traps near a stream "Rio Esmeraldas". Adult males and females were collected in the same pitfall line but during a different period.

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I sincerely thank the following people; Elicio Tapia and César Tapia for their help in the field. To Dr. Giovanni Onore and Dr. Luis Coloma for their support through Otonga foundation and their work in studying and protecting Ecuador's biodiversity. I am grateful to National Geographic which funded this study, "Spider diversity of the cloud forest in the Chocó region of Ecuador ", through the Waitt Grant program (W294-13). The collection of specimens was done under a permit (No 006-14IC-FAU-DNB/MA) of the Ministerio de Ambiente, Quito, Ecuador.

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Description of two new species of *Tangaroa* Lehtinen 1967 (Arachnida: Araneae: Uloboridae)

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Abstract. Two new species of *Tangaroa* Lehtinen 1967 (Araneae: Uloboridae) from the Cook Islands are described here: *Tangaroa vaka* **n. sp.** from Rarotonga, and *Tangaroa pukapukan* **n. sp.** from Mitiaro, both based on male and female specimens.

Keywords: Spiders, Haplogynae, cribellate spider, Deinopoidea

Tangaroa Lehtinen 1967 is a genus of cribellate orb weaver spiders belonging to the family Uloboridae. It is recognized by the presence of six eyes; the members of this group have lost the anterior lateral eyes, having a pair of small pigment spots instead. Males have a distal crook on the ventral surface of tibia I, a simple palpus with a flattened embolus and no sclerite guides, a stridulatory apparatus on the endites, and females are considered secondary haplogyne (Opell 1979, 1983).

Tangaroa was erected by Lehtinen (1967) to include the type-species *T. tahitiensis* (Berland 1934) from Rapa, Tahiti, and *T. dissimilis* (Berland 1924) from New Hebrides, New Caledonia, both species transferred from *Uloborus* Latreille 1806. In 1983, Opell revised the genus, described a third species, *T. beattyi* Opell 1983 from the Caroline Islands, Philippines, and also provided a cladistic hypothesis with the three species reviewed based on fifteen morphological characters, where nine of those were scored based on the presence and position of macrosetae.

A phylogenetic study published by Coddington (1990) supported *Tangaroa* as a sister group of the monotypic *Waitkera* Opell 1979 and, based on the primitive state of its palp, *Tangaroa* was also proposed as the basal uloborid rather than *Waitkera* as suggested by Opell (1979).

The collection of the California Academy of Science was examined during a visit by the first author. Two new species of *Tangaroa* were recognized from the Cook Islands, one from Rarotonga, and other from Mitiaro. Both are described in this paper, with detailed illustrations of diagnostic characters.

METHODS

The material was deposited in the collection of the California Academy of Sciences, California (curator: C. Griswold). Descriptions and morphological terminology follows Opell (1979). The specimens were kept in 80% ethanol and examined under Leica MZ AP0 stereoscopy. Internal tissues of epigynes were digested with pancreatin and cleared with methyl salicylate. Palpi were also cleared with methyl salicylate. For the Scanning Electron micrographs (LEO 1430VP), both sexes' genitalia were cleaned ultrasonically for 1–3 minutes, and after critical point drying (Autosandri-815), the structures were mounted and sputter coated with gold (Denton Vacuum). The specimens were photographed using a Leica M205A stereoscopic microscope equipped with a Leica DFC425 camera and LAS software, and also some images were refined using Helicon Focus (version 5.3; www.heliconsoft.com) software from Helicon Soft Ltd. The images were edited in Adobe Photoshop CS3. For the illustrations, images were used as templates to trace vector graphics in Adobe Illustrator CS4 (version 14.0.0). The measurements are in millimeters and were taken under various magnifications using a Leica MZ AP0. Abbreviations: ALE — Anterior Lateral Eyes; AME — Anterior Median Eyes; cd — Copulatory ducts; el — Embolar lobe; Go — Gonopore; mb — Microbarbs; pg — Pore glands; PLE — Posterior Lateral Eyes; PME — Posterior Median Eyes; S — Spermathecae heads; Ue — Uterus externus.

TAXONOMY

Tangaroa Lehtinen 1967

Tangaroa Lehtinen 1967: 266. Type species *Uloborus tahitiensis* Berland 1934, by original designation.

Tangaroa vaka new species

Type Material.—Holotype: male from Cook Islands, Rarotonga, 21°13′57.9″ S, 159°45′57.5″ W, 15-18.I.1996, J. Boutin col., deposited in CAS. **Paratypes:** two males and three females, same data as holotype.

Etymology.—The specific epithet means "canoe" in the common language of the Polynesian Islands and it was an important transportation used by natives in Cook Islands. The vaka have a symbolic significance to the Polynesian society symbolizing the interconnectedness of the village, the sea, the Earth and the Heavens.

Diagnosis.—Males of this species are distinguished from other *Tangaroa* species by the first leg having three macrosetae in or adjacent to the ventral tibial notch (Figs. 1e, 9g), two prolateral femoral macrosetae, and five dorsal tibial macrosetae. Also differs from *T. dissimilis* and *T. beattyi* by

Figure 1.—*Tangaroa vaka* n. sp. a. female, dorsal view; b. male, dorsal view; c. femur IV, calamistrum, prolateral view, female; d. carapace, lateral view, male; e. femur I, distal crook (arrow), retrolateral view. Scale bars: a, b. 1 mm; c, d. 0.2 mm; e. 0.5 mm.

the rounder than ovoid tegulum (Figs. 3a, 9a); from *T. beattyi* by lacking a cymbial notch (Fig. 9a); and, from *T. pukapukan* n. sp., by lacking microbarbs on the embolus and lacking a lobe on base portion of the embolus (Fig. 9c, d, f). Females are characterized by having one prolateral and one retrolateral macrosetae on femur I, by the shape of the spermathecae and the interdistance between spermathecae being more than twice the spermathecae diameter (Fig. 2c, e). Also differs from *T. dissimilis* by having genital macrosetae (Fig. 2a); from *T. beattyi* by lacking an elongated pigmentation of the PMEs (Fig. 1a); and from *T. pukapukan* n. sp. by lacking a notch on the posterior margin of the epigynum (Fig. 2a).

Description.—**Male (holotype): Carapace:** Total length 3.58, carapace 1.20 long, 1.01 wide; yellow (Fig. 1b, d); shallow fovea. **Eyes:** AME on anterior elevation. Eye diameter: AME = PE, ALEs small pigment spots. Distance between eyes: AME–AME, 0.20; ALE–ALE, 0.40; PLE–PLE, 0.52; PME–PME, 0.20; PME–PLE, 0.10; AME–ALE, 0.06. **Clypeus:** AME–clypeus, 0.18. **Mouthparts: Endites** with stridulatory file formed of about 16 rows of denticles (Fig. 7a–c); serrula present (Fig. 7d); 0.31 long, 0.25 wide; light yellow. **Labium** 0.22 long, 0.20 wide; light yellow. **Chelicerae** light yellow; cheliceral fang with teeth (Fig. 8a, b), and cheliceral groove smooth with two rows of teeth (Fig. 8h), 23 retrolateral teeth, 27 prolateral teeth (Fig. 8c, d). **Sternum:** 0.68 long, 0.58 wide; light yellow. **Pedipalp:** light yellow. **Legs:** Ventrolateral stridulatory picks on proximal portion of femur I (Fig. 6a, b); yellow; formula 1423; **I:** femur 2.48, patella 0.62, tibia 2.48, metatarsus 2.64, tarsus 1.00, total 9.22. **II:** 1.40, 0.48, 1.18, 1.28, 0.62, 4.96. **III:** 1.07, 0.31, 0.69, 0.86, 0.49, 3.42. **IV:** 1.74, 0.39, 1.30, 1.33, 0.81, 5.57. Calamistrum absent. **Abdomen:** 2.38 long, 1.13 wide; abdomen dorsally pale white, posterior and lateral margin with darker patches; ventrally pale white with genital area and spinnerets darker (Fig. 1b). **Palpus:** as in Fig. 3a–e; cymbium with two spines on distal margin

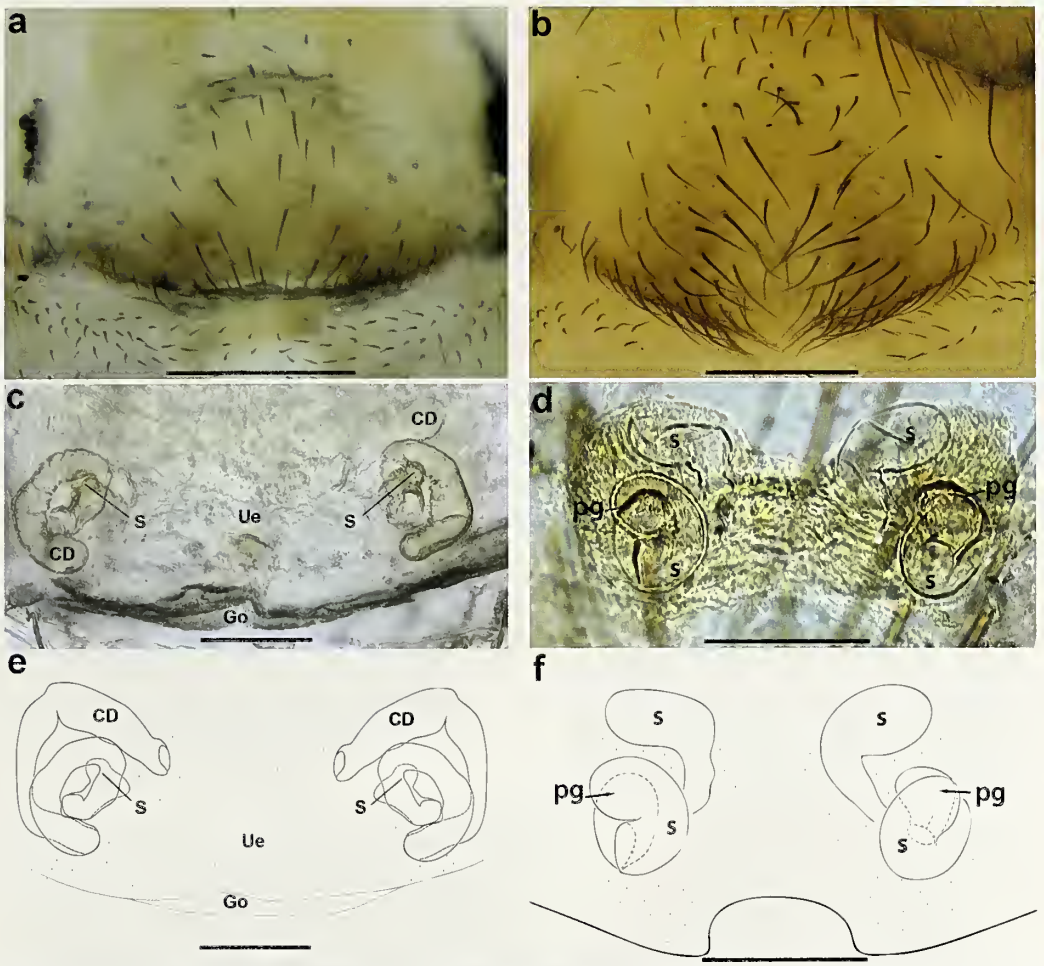

Figure 2.—a–c. *Tangaroa vaka* n. sp., female, epigynum. a. Ventral view; b. cleared, dorsal view; c. dorsal view. d–f. *Tangaroa pukapukan* n. sp., female, epigynum. d. Ventral view; e. cleared, dorsal view; f. dorsal view. Scale bars: a, 0.3 mm; b, c, e, f, 0.1 mm; d, 0.2 mm.

(Fig. 9b); embolus long and flattened, except at tip (Fig. 9f); not associated with a conductor, but the basal area in a tegular sulcus (Fig. 3a, d)

Female (paratype): Carapace: Total length 4.50, carapace 1.40 long, 1.02 wide; pale yellow with darker paramedian bands (Fig. 1a). Shallow fovea. **Eyes:** as in males, except AME not on anterior elevation. Distance between eyes: AME–AME, 0.20; ALE–ALE, 0.44; PLE–PLE, 0.60; PME–PME, 0.26; PME–PLE, 0.05; AME–ALE, 0.04. **Mouthparts: Endites** 0.34 long, 0.31 wide; light yellow. **Labium** 0.20 long, 0.23 wide; light yellow. **Chelicerae** as in male; pale yellow. **Sternum:** 0.74 long, 0.54 wide; yellow. **Pedipalp:** pale yellow; claw with ten teeth. **Legs:** pale yellow; formula 1423; **I:** femur 2.79, patella 0.71, tibia 2.60, metatarsus 2.72, tarsus 1.05, total 9.87. **II:** 1.63, 0.53, 1.18, 1.53, 0.75, 5.62. **III:** 1.30, 0.30, 0.83, 1.00, 0.58, 4.01. **IV:** 2.17, 0.53, 1.65, 1.70, 1.18, 7.23. Calamistrum present (Fig. 1c). **Abdomen:** 3.10 long, 1.49 wide; abdomen dorsally pale white with darker patches; lateral margin darker; ventrally pale white (Fig. 1a). **Epigynum:** no modification externally (Fig. 2a); one pair of weakly sclerotized, elongated and coiled spermathecae with two inconspicuous spermathecae heads and pores glands (Fig. 2c, e).

Variation.—Cephalothorax length: males (n = 3): 1.20–1.30; females 1.17–1.40. Total body length: males (n = 3): 3.31–3.71; females (n = 2): 4.07–4.50. Femur I, males (n = 3): 2.38–2.61; females (n = 3): 2.43–2.79.

Distribution.—Known only from Rarotonga, Cook Islands.

Tangaroa pukapukan new species

Type Material.—Holotype: male from Cook Islands, Mitiaro, 19°52′45.1″ S, 157°42′23.1″ W, 19-21.I.1996, J. Boutin col., deposited in CAS. **Paratypes:** three males and three females, same data as holotype.

Etymology.—The specific name refers to one of the spoken languages in the Cook Islands.

Diagnosis.—Males are distinguished from other *Tangaroa* species by the distal crook strongly marked (Fig. 10c), embolus with three microbarbs (Fig. 10d–f), the basal portion of the embolus with a lobe (Fig. 10a, b) and first leg having three or four macrosetae in or adjacent to the ventral tibial notch (Fig. 4e), two prolateral femoral macrosetae and five dorsal tibial macrosetae. Also differs from *T. beattyi* by lacking a cymbial notch. Females are characterized by having a notch on the posterior margin of the epigynum (Fig. 2b, f),

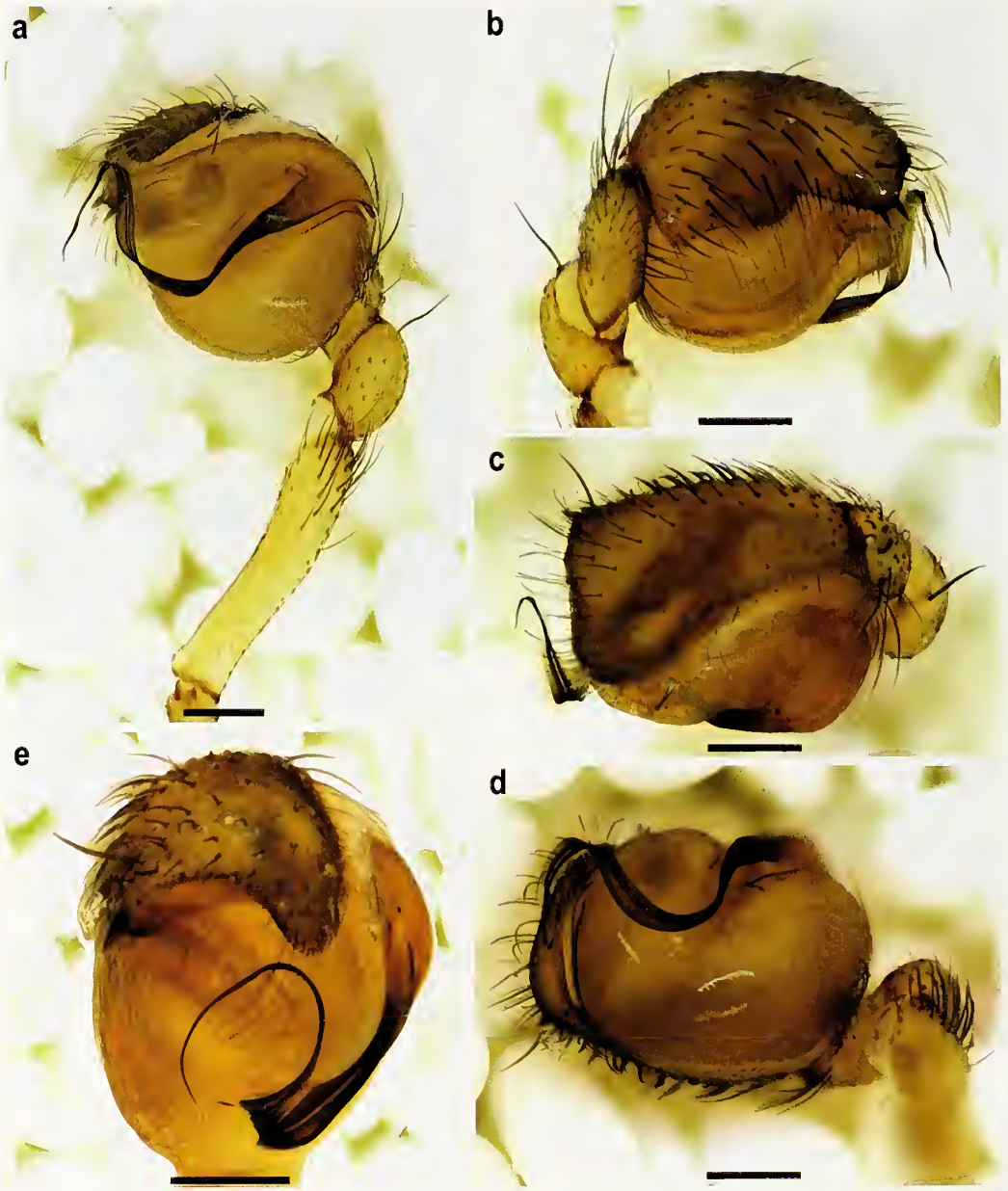

Figure 3.—*Tangaroa vaka* n. sp., palp. a. Prolateral view; b. retrolateral view; c. dorsal view; d. ventral view; e. frontal view. Scale bars, 0.2 mm.

by the shape of the spermathecae (Fig. 2d, f) and one prolateral and two retrolateral macrosetae on femur I. Also differs from *T. dissimilis* by having genital macrosetae; differs from *T. beattyi* by the absence of an elongated pigmentation of the PMEs.

Description.—**Male (holotype): Carapace:** Total length 3.20, carapace 1.20 long, 1.00 wide; pale yellow (Fig. 4b); shallow fovea. **Eyes:** AME on anterior elevation. Eye diameter: AME = PE, ALEs small pigment spots. Distance between eyes: AME–AME, 0.20; ALE–ALE, 0.39; PLE–PLE, 0.56; PME–PME, 0.20; PME–PLE, 0.08; AME–ALE, 0.08. **Clypeus:** AME–clypeus, 0.16. **Endites** with stridulatory file formed of about 16 rows of denticles (Fig. 7e–h); serrula present (Fig. 7g); 0.33 long, 0.25 wide; light yellow. **Labium** 0.23 long, 0.21 wide; light yellow. **Chelicerae** light yellow; cheliceral fang with teeth (Fig. 8e); cheliceral groove smooth with two rows of teeth, 25 retrolateral teeth, 24 prolateral teeth (Fig. 8g, h). **Sternum:** 0.63 long, 0.53 wide; pale yellow. **Pedipalp:** pale yellow. **Legs:** Ventrolateral stridulatory picks on proximal portion of Femur I (Fig. 6c–f); pale yellow; formula 1423; **I:** femur 2.00, patella 0.58, tibia 2.02, metatarsus 2.05, tarsus 0.90, total 7.55. **II:** 1.15, 0.45, 1.00, 1.05, 0.55, 4.20. **III:** 0.80, 0.25, 0.60, 0.75, 0.48, 2.88. **IV:** 1.33, 0.40, 1.13, 1.08, 0.83, 4.77. Calamistrum absent. **Abdomen:** 2.00 long, 1.00 wide; abdomen dorsally pale white, posterior and lateral margin with darker patches; ventrally pale white with genital area and spinnerets

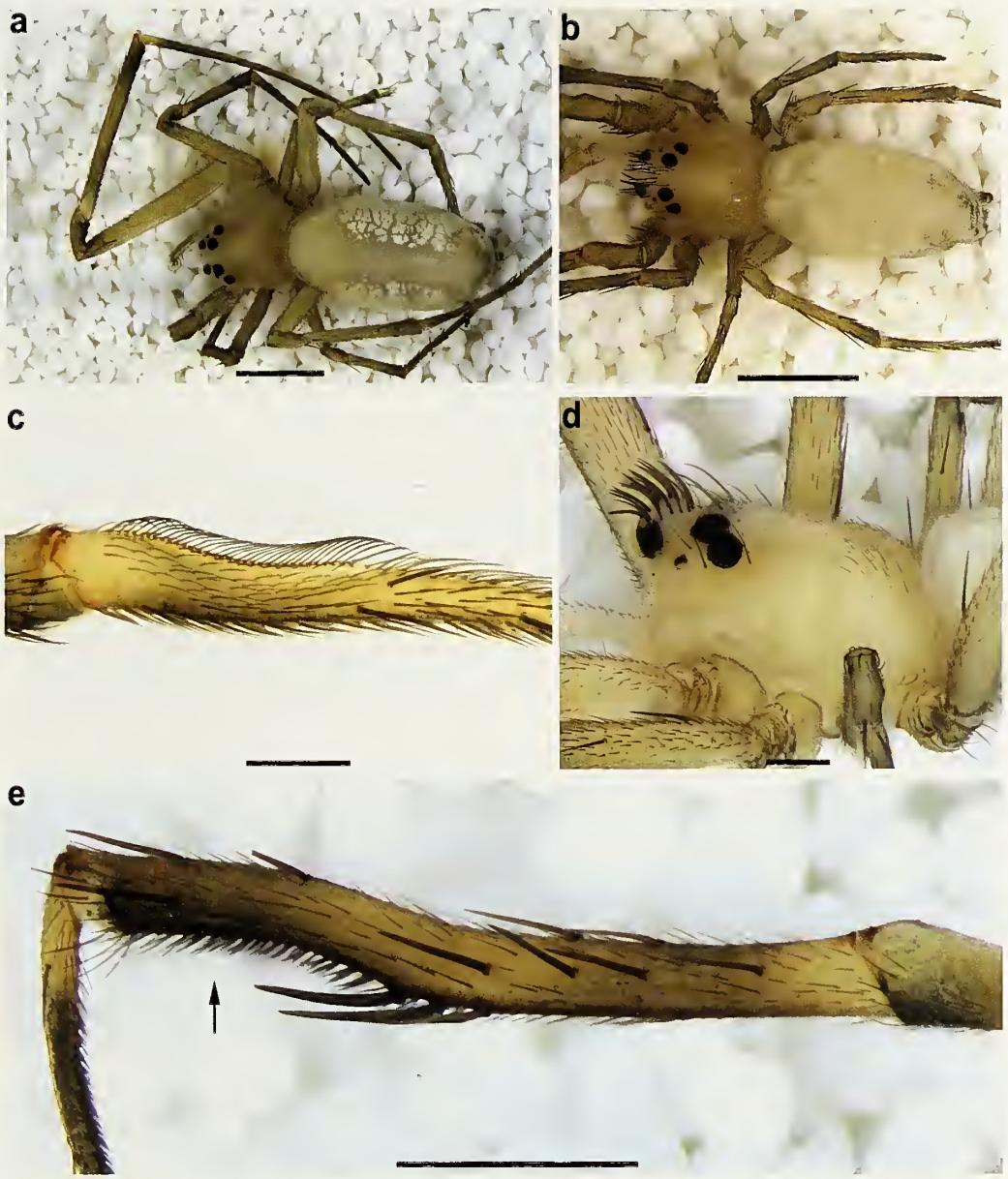

Figure 4.—*Tangaroa pukapukan* n. sp. a. Dorsal view, female; b. dorsal view, male; c. femur IV, calamistrum, prolateral view, female; d. carapace, lateral view, male; e. femur I, distal crook (arrow), retrolateral view. Scale bars: a, b, 1 mm; c, d, 0.2 mm; e, 0.5 mm.

darker (Fig. 4b). **Palpus:** as in Figs. 5a–e and 10a, b, d–h; cymbium longer than wide, with two spines on distal margin (Fig. 5b); embolus long and flattened, with tip coiled and enlarged base (Fig. 10g, h), not associated with a conductor, but the basal area in a tegular sulcus (Fig. 5d, e).

Female: Carapace: Total length 4.76, carapace 1.25 long, 1.05 wide; pale yellow (Fig. 4a); Shallow fovea. **Eyes:** as in males, except AME not on anterior elevation. Distance between eyes: AME–AME, 0.19; ALE–ALE, 0.45; PLE–PLE, 0.59; PME–PME, 0.25; PME–PLE, 0.11; AME–ALE, 0.05. **Mouthparts:** Endites 0.31 long, 0.26 wide; light yellowish green. Labium 0.25 long, 0.24 wide; dark yellowish green. **Chelicerae** as in male, 28 retrolateral teeth and 32 prolateral teeth (Fig. 8g, h); pale yellow. **Sternum:** 0.81 long, 0.56 wide; pale yellow with margin darker. **Pedipalp:** pale yellow; claw with ten teeth. **Legs:** pale yellow; formula 1423; **I:** femur 2.54, patella 0.68, tibia 2.45, metatarsus 2.54, tarsus 0.96, total 9.17. **II:** 1.30, 0.50, 1.13, 1.18, 0.63, 4.74. **III:** 1.25, 0.38, 0.75, 0.95, 0.58, 3.91. **IV:** 1.80, 0.50, 1.50, 1.33, 0.88, 6.01. Calamistrum present (Fig. 4c). **Abdomen:** 3.51 long, 2.02 wide; abdomen dorsally pale white; white guanine spots scattered throughout length dorsally/laterally; lateral margin pale white; ventrally pale white (Fig. 4a). **Epigynum:** no modification externally (Fig. 2b); one pair of weakly sclerotized, elongated spermathecae with two conspicuous spermathecae heads and pores glands (Fig. 2d, f).

Variation.—Ocular macrosetae varies from 27 to 38 in males. Carapace length, males (n = 4): 1.20–1.25; females

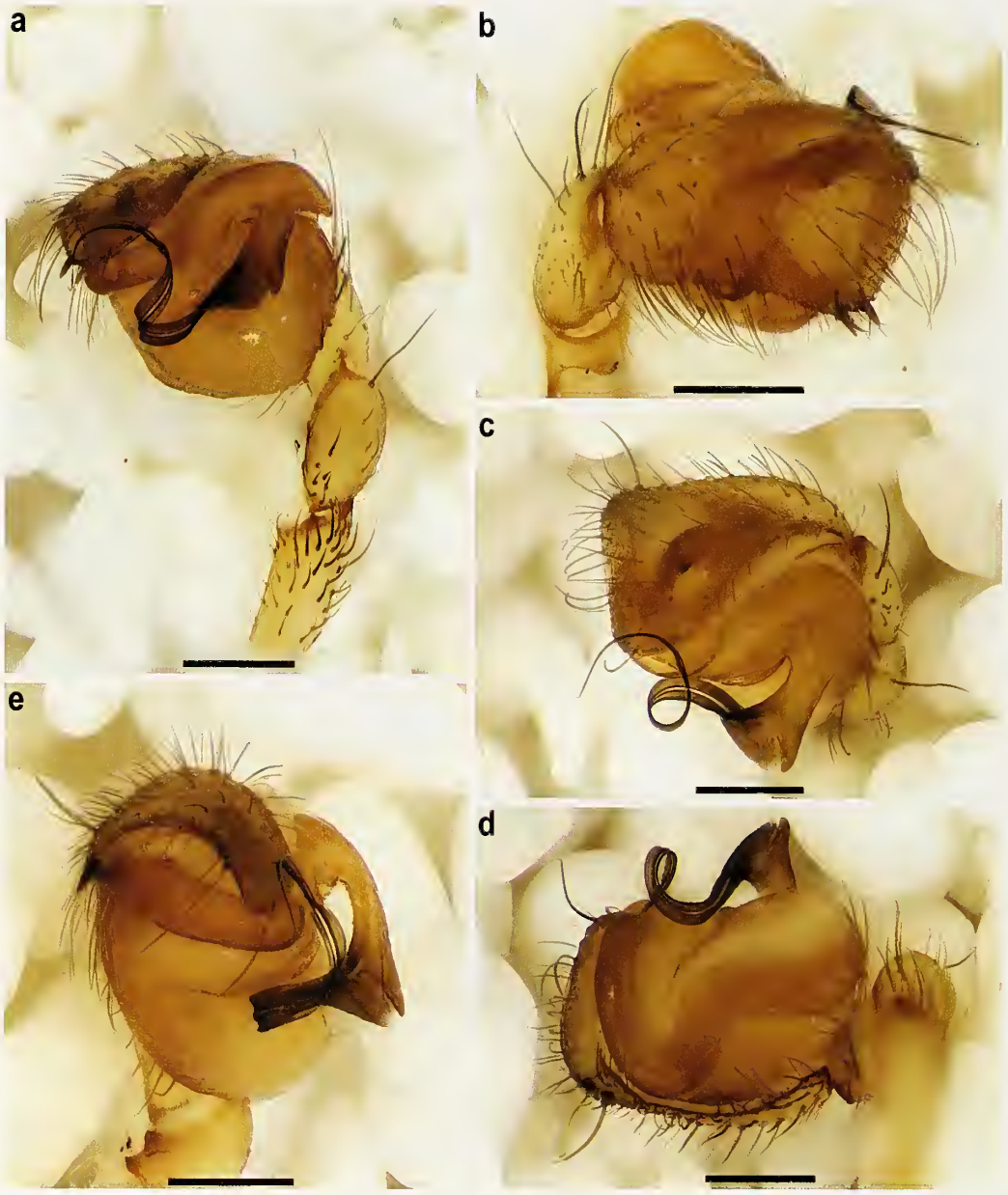

Figure 5.—*Tangaroa pukapukan* n. sp., palp, cleared. a. Prolateral view; b. retrolateral view; c. dorsal view; d. ventral view; e. frontal view. Scale bars: a–e, 0.2 mm.

(n = 3): 1.15–1.25. Total body length, males (n = 4): 3.19–3.35; females (n = 3): 3.92–4.90. Femur I, males (n = 4): 2.00–2.15; females (n = 3): 2.50–2.57.

Distribution.—Known only from Mitiaro, Cook Islands.

DISCUSSION

The morphology of the genitalia of both *Tangaroa vaka* and *T. pukapukau* is typical for the *Tangaroa* species with an elongated tubule with two distinctive spermathecae heads with pore glands in the middle portion of the tubule and close to the copulatory ducts (Opell 1983). Opell (1983) briefly discussed the hypothesis about the dynamics of sperm storage using histological section observations in *Tangaroa* species.

It is known that spider sperm are non-motile at copulation time (Baccetti et al. 1970), and that males are prevented from directly depositing sperm into the storage sacs by the length and width of the insemination duct, and also by its own organ size (Watson 1991; Huber 1993). It is also known that lengthening the duration of copulation is a form of fertilization strategy, since sperm release can be time-dependent (Watson & Lighton 1994; Szirányi et al. 2005) and the advantage in fertilization goes to the male with the greatest number of sperm within the female's reproductive

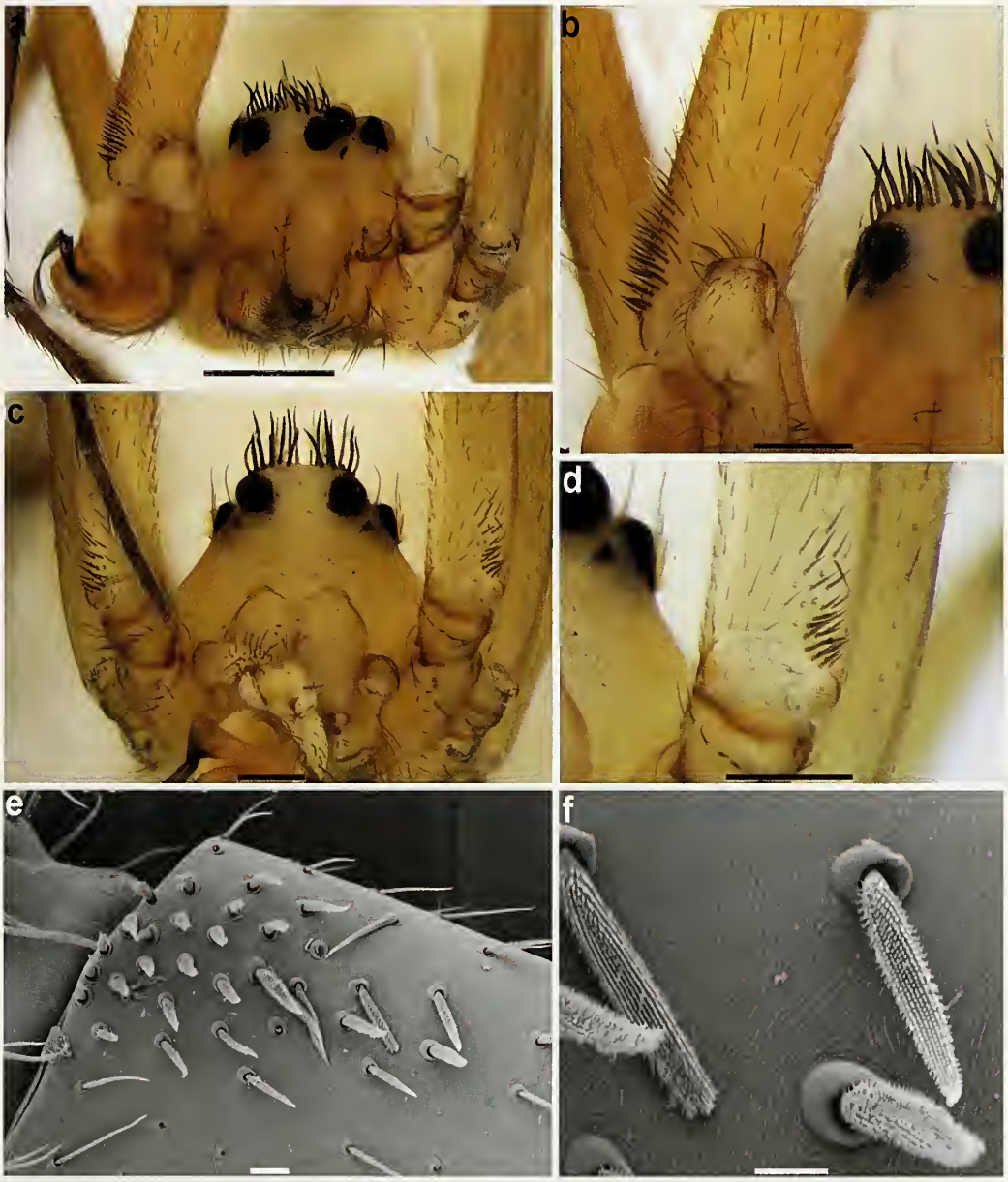

Figure 6.—a. *Tangaroa vaka* n. sp., male. frontal view; b. stridulatory picks on femur I; c. *Tangaroa pukapukan* n. sp., male. frontal view; d. stridulatory picks on femur I; e. same; f. detail of a stridulatory pick. Scale bars: a, 0.5 mm; b–d, 0.2 mm; e, 0.02 mm; f, 0.01 mm.

tract and how close the sperm are to the fertilization duct (Uhl & Vollrath 1998).

In the males of *Tangaroa*, the embolus of the male is quite long, which might be an advantage during the insemination. The length of the embolus could help the initial transport of the sperm inside the genitalia ducts by providing a deeper release of the sperm into the female receptacles. Also the lack of a conventional conductor might help to produce a deep insertion. This might reduce the need of a time-consuming copulation. The strategy of a deep release of the sperm suggests that the internal transport of the sperm in *Tangaroa* is not completely dependent on the female.

In addition, microbarbs were observed along the middle portion of the embolus in males of *T. pukapukan* (Fig. 10d–h), which may function as anchors during mating, to aid the male in staying attached to the female. Studies regarding the courtship and mating behavior (female resistance behaviors, intrasexual competition and postcopulatory function of genitalia) of *Tangaroa* species are needed to identify the function of the microbarbs.

Also, some slight differences in the stridulatory apparatus of the two new species and *T. beattyi* were observed. In *T. vaka* (Fig. 7b) the ridges of the stridulatory apparatus are twice as wide and more numerous, with a difference of four to six more

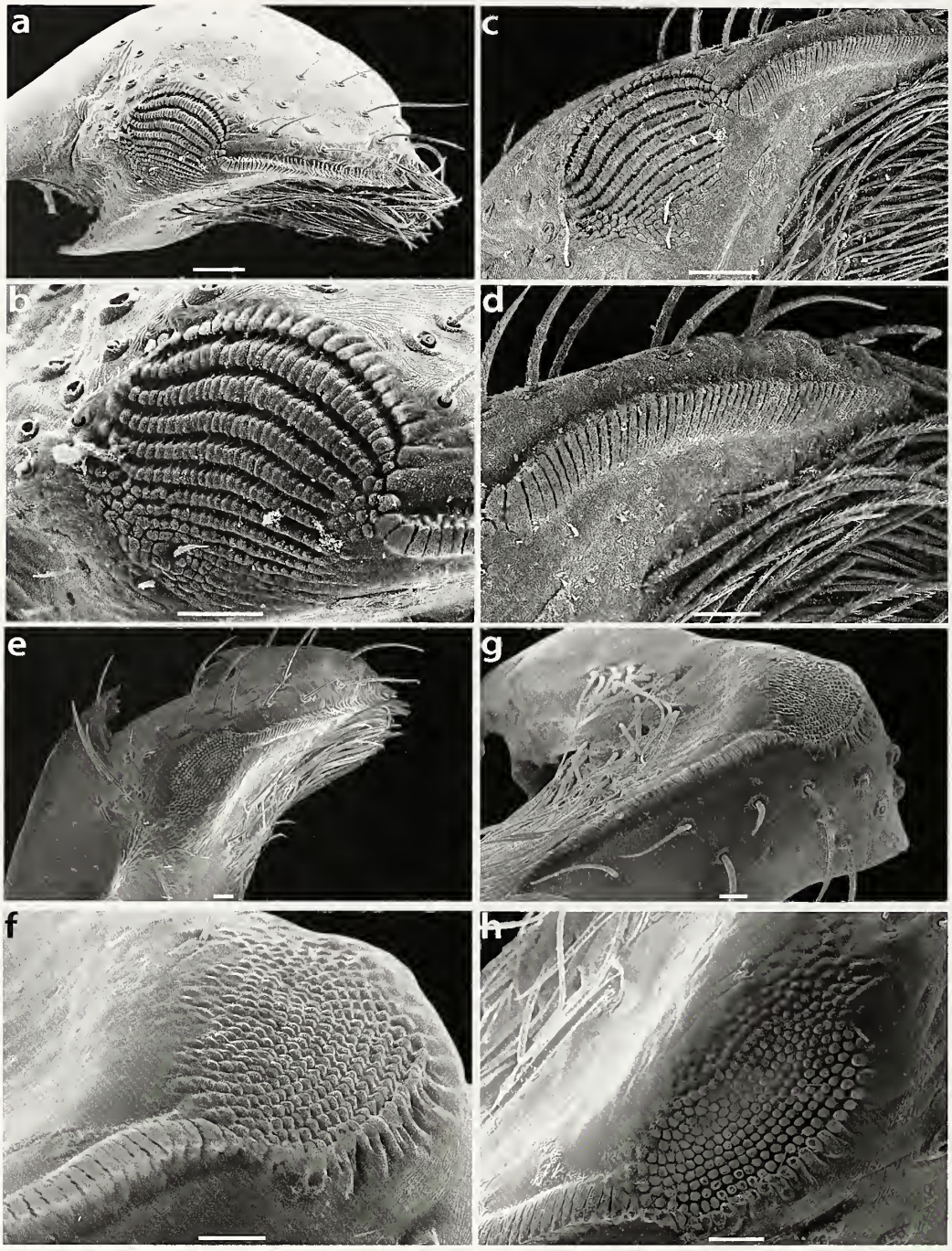

Figure 7.—a–d. *Tangaroa vaka* n. sp., male, endite. a. Endite, dorsolateral view; b. details of stridulatory file; c. stridulatory file and serrula, dorsal view; d. details of serrula. Scale bars: a, 0.04 mm; b, d, 0.02 mm; c, 0.03 mm. e–h. *Tangaroa pukapukan* n. sp., male, endite. e. Endite, dorsolateral view; f–g. stridulatory file and stridulatory file, dorsolateral view; h. details of stridulatory file, dorsal view. Scale bars: e–h. 0.01 mm.

ridges per line than in *T. pukapukan* (Fig. 7f–h) and, a difference of three to seven fewer ridges per line in *T. beattyi* (Opell 1983: fig. 1). The form of the ridges is similar in *T. pukapukan* and *T. beattyi*. The number of stridulatory rows varies from 13 in *T. pukapukan*, 14 in *T. vaka* and 17 in *T. beattyi*.

On the prolateral portion of the femur I on males of both new species a series of modified distal setae are present (Fig. 6a–d). The SEM images of these setae show that they are a wide, thickened, unilaterally and strongly barbed, spatulate type of setae (Fig. 6e, f). These setae might also act as a scraper. The plectrum in *Tangaroa* species was suggested by

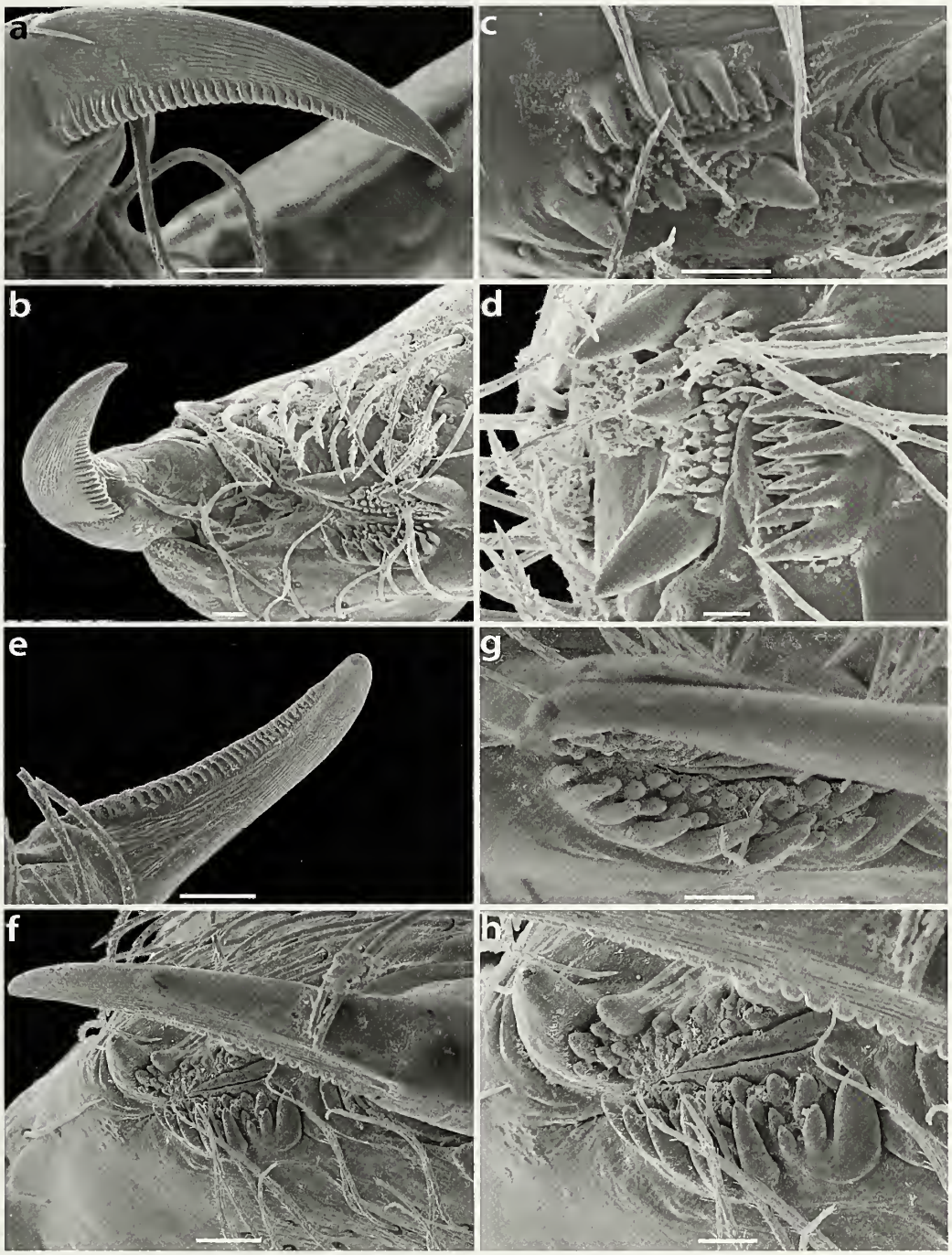

Figure 8.—a–d. *Tangaroa vaka* n. sp., chelicerae. a. Dorsal view; b–d. details of cheliceral teeth. e–f. *Tangaroa pukapukan* n. sp., chelicerae. e. Retrolateral view; f–h. details of cheliceral teeth. Scale bars: a—h, 0.02 mm.

Opell (1983) to be the setal picks on the cymbium and it is present in both new species.

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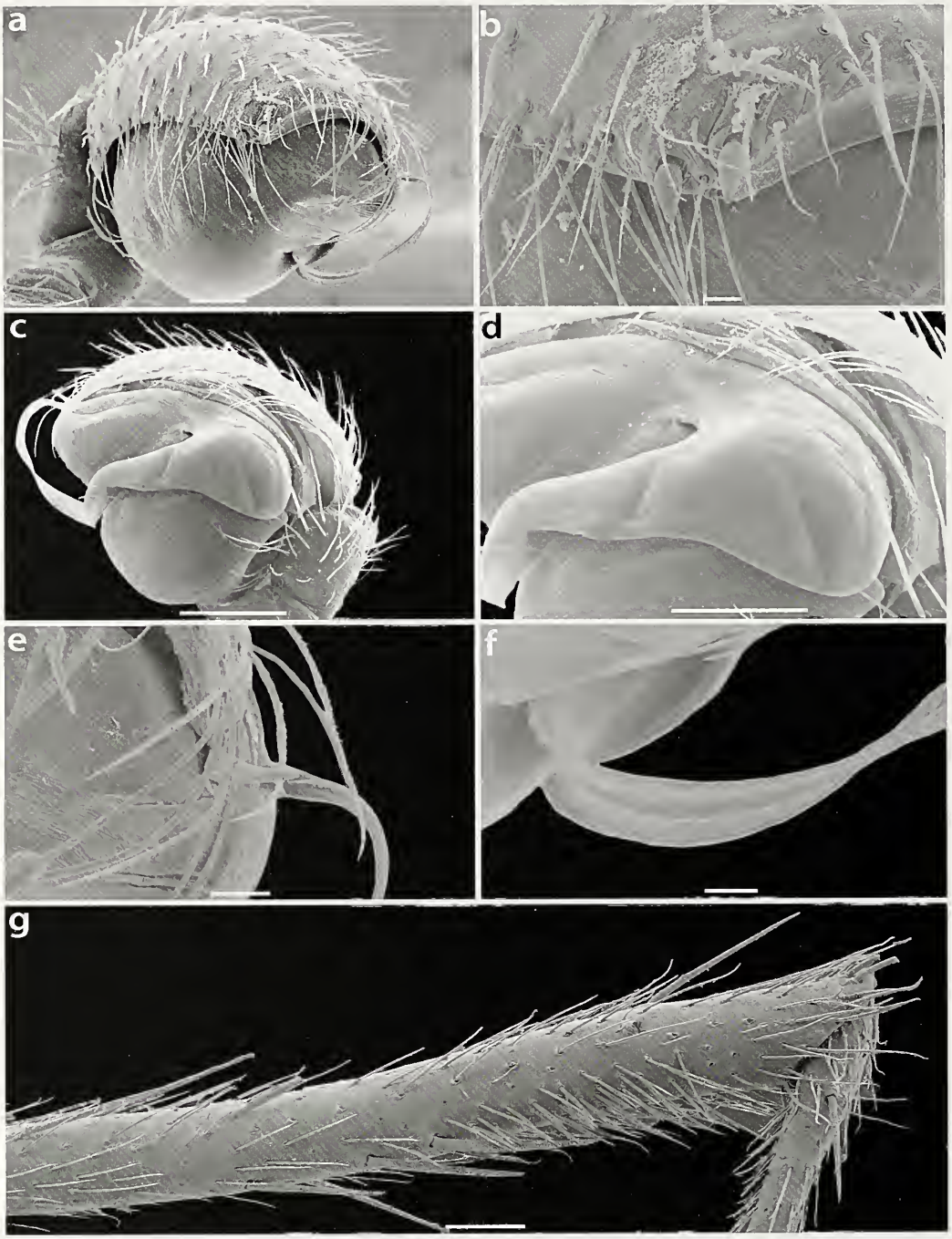

Figure 9.—*Tangaroa vaka* n. sp., palp, male. a. Retrolateral view; b. cymbial spines; c. prolateral view; d. distal portion of embolus; e. apical portion of embolus; f. median portion of embolus; g. femur I, distal crook, retrolateral view. Scale bars: a,d,g, 0.1 mm; b, e, f, 0.02 mm; c, 0.2 mm.

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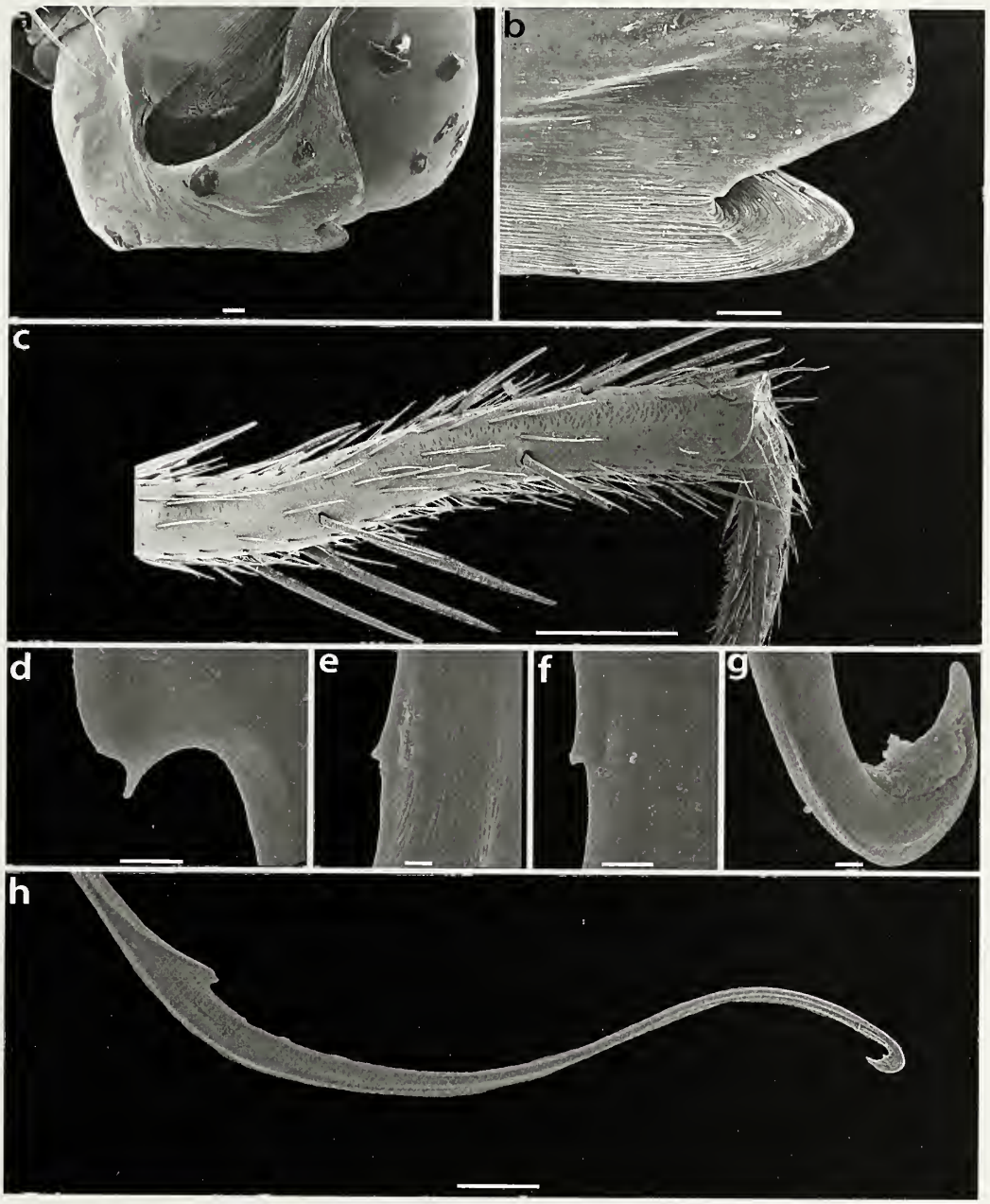

Figure 10.—a–c. *Tangaroa pukapukan* n. sp., palp. a. Distal portion of embolus; b. details of distal portion of embolus; c. femur I, distal crook, retrolateral view. d–h. *Tangaroa pukapukan* n. sp., palp, male. d–f. Microspines of embolus; g. apical portion of embolus; h. embolus. Scale bars: a, c–g, 0.02 mm; b, h, 0.01 mm.

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A review of the taxonomy and biology of pseudoscorpions of *Nannowithius* and *Termitowithius* (Pseudoscorpiones, Withiidae), inquilines of social insects

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Abstract. The *Nannowithius* group of the pseudoscorpion family Withiidae is newly defined, consisting of *Nannowithius* Beier, 1932 from northern Africa and the Middle East, and *Termitowithius* Muchmore, 1990 from east Africa. The group is characterized by the lack of a tactile seta on the posterior tarsi, and they are the only withiids to possess this character state. Both genera are associated as inquilines with social insects, *Nannowithius* with ants and *Termitowithius* with termites. *Withius caecus* Beier, 1929 and *Plesiowithius dekeyseri* Vachon, 1954 are redescribed and transferred to the genus *Nannowithius*, forming the new combinations *N. caecus* (Beier) and *N. dekeyseri* (Vachon). *Plesiowithius* is treated as a new synonym of *Nannowithius*. A revised description and new illustrations of *Termitowithius kistneri* Muchmore, 1990 are presented.

Keywords: Taxonomy, morphology, new synonymy

Many different pseudoscorpions have been recorded in the nests of social insects, termites, bees and ants. However, many of these records are rather circumstantial and based on collecting records, rather than any detailed examination of the biology of the pseudoscorpion and its association with its host. In most cases, the pseudoscorpions are species that occur in other habitats, and their association with insects is fortuitous or, at best, temporary.

Perhaps the best documented example is the association between species of the cheliferid genus *Ellingsenius* Chamberlin, 1932 and bees in Africa, Asia and southern Europe; there are virtually no records of *Ellingsenius* being collected anywhere other than bee nests. Likewise, species of the chernetid genus *Dasychernes* Chamberlin, 1929 are known from bee nests in Central America (Chamberlin 1929; Gonzalez et al. 2008). The Australian genus *Marachernes* Harvey, 1992 is associated with ants of the genus *Anonychomyrma* Donisthorpe (Harvey 1992a; Cole et al. 1995). The sole species of *Myrmochernes* Tullgren, 1907, *M. africanus* Tullgren, 1907 occurs with *Camponotus maculatus* (Fabricius, 1782) in South Africa (Tullgren 1907). The three species of *Sphenochernes* Turk, 1953 have been found in ants' nests, with *S. bruchi* Mello-Leitão, 1925 and *S. schulzi* Turk, 1953 from Argentina associated with *Acromyrmex hundii* Guérin-Méneville, 1838 (Mello-Leitão 1925; Turk 1953), and *S. camponoti* (Beier, 1970) with *C. rufipes* (Fabricius, 1775) in southern Brazil (Beier 1970). Another genus that is strongly associated with social insects is the African chernetid genus *Pilanus* Beier, 1930, with *P. pilatus* Beier, 1930 from Senegal and *P. pilifer* Beier, 1930 from Eritrea found in termite nests (Beier 1930), and *P. proximus* Beier, 1955 from a nest of the ant *Messor cephalotes* (Emery, 1895) in Kenya (Beier 1955a). Other species associated with termites are relatively rare, but the best known association is the bizarre African termitophile *Termitowithius kistneri* Muchmore, 1990 of the family Withiidae (Muchmore 1990), although other pseudoscorpions are known to inhabit the abandoned nests of termites (e.g., Girard & Lamotte 1990; Heurtault 1994; Martius et al. 1994).

While examining specimens of the family Withiidae, major similarities between the genera *Termitowithius* and *Nannowithius* Beier, 1932 were noted, which were also shared with the genus *Plesiowithius* Vachon, 1954. These resemblances may indicate a common ancestry. The purposes of this paper are to provide a redescription of some species of *Nannowithius* and *Termitowithius*, to transfer *Withius caecus* Beier, 1929 to *Nannowithius*, and to examine the relationship of *Plesiowithius* with *Nannowithius*.

METHODS

The material mentioned in this study is lodged in the Florida State Collection of Arthropods, Gainesville (FSCA), Hungarian Natural History Museum, Budapest (HNHM), Hebrew University of Jerusalem (HUJ), Museo Civico di Storia Naturale di Genova (MCSNG), Muséum d'histoire naturelle de la Ville de Genève (MHNG), Museum National d'histoire Naturelle, Paris (MNHN), Museo Zoologio di Università degli Studi di Napoli, Portici, Italy (MZUN), Naturhistorisches Museum Basel (NMB), and Naturhistorisches Museum Wien (NHMW). The specimens stored in ethanol were examined by preparing temporary slide mounts by immersing the specimen in 75% lactic acid at room temperature for several days, and mounting them on microscope slides with 10 mm coverslips supported by small sections of 0.25 mm diameter nylon fishing line. Specimens were observed with a Leica DM2500 compound microscope and illustrated with the aid of a drawing tube. Measurements were taken at the highest possible magnification using an ocular graticule. After study, the specimens were rinsed in water and returned to 75% ethanol with the dissected portions placed in 12 x 3 mm glass genitalia microvials (BioQuip Products, Inc.).

Terminology and mensuration mostly follow Chamberlin (1931), with the exception of the nomenclature of the pedipalps and legs, and with some minor modifications to the terminology of the trichobothria (Harvey 1992b), cheliceral setation (Harvey & Edward 2007), cheliceral rallum (Judson 2007)

and faces of the appendages (Harvey et al. 2012). The ratio TS is the distance from the base of tarsus IV to the tactile seta, divided by the length of the entire tarsus. The abbreviation gls refers to the abdominal glandular setae found on the sternites of many withiids. The following abbreviations are used for the male genitalia: ca, chitinized arch; ejca, ejaculatory canal atrium; la, lateral apodeme; pvd, postero-ventral diverticulum; vd, ventral diverticulum.

Only the original description is given in the synonymy of each taxon; other citations can be found in Harvey (2013).

SYSTEMATICS

Family Withiidae Chamberlin, 1930
Genus *Nannowithius* Beier, 1932

Nannowithius Beier 1932:57.
Plesiowithius Vachon 1954:1029. **Syn. nov.**
Myrmecowithius Beier 1963: 195–196 (synonymized by Mahnert 1988:68).

Type species.—*Nannowithius: Chelifer aethiopicus* Simon, 1900, by original designation.

Plesiowithius: Plesiowithius dekeyseri Vachon, 1954, by original designation.

Myrmecowithius: Myrmecowithius wahrmani Beier, 1963, by original designation.

Diagnosis.—Species of *Nannowithius* differ from all other withiids, except *Termitowithius kistneri*, by the lack of a tactile seta on the tarsi of legs III and IV. *Nannowithius* differs from *Termitowithius* by the presence of a venom apparatus in both chelal fingers (vestigial in *Termitowithius*), the presence of abdominal glandular setae (absent in *Termitowithius*), the lack of numerous sense spots on the chelal fingers (present in *Termitowithius*), and the presence of paired spermathecae (spermathecae absent in *Termitowithius*).

Description.—*Adults:* Chelicera: with 5 setae on hand and 1 subdistal seta on movable finger; seta *bs* and *sbs* dentate, remaining setae acuminate; seta *bs*, *sbs* and *es* shorter than others; rallum of 4 blades, the most distal blade with several serrations on leading edge, other blades smooth.

Pedipalp: Chelal fingers elongated. Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria: *est* situated closer to *et* than to *esb* or midway between *esb* and *et*; *it* situated subdistally; *st* situated closer to *t* than to *sb*; *sb* situated much closer to *b* than to *st*. Retrolateral margin of chelal fingers without numerous sensilla. Venom apparatus present in both chelal fingers, nodus ramosus slightly inflated.

Carapace: Eyes present (as vestigial eye-spots) or absent; with 2 furrows, posterior furrow situated closer to posterior carapace margin than to anterior furrow.

Legs: junction between femora and patellae I and II slightly oblique to long axis; tarsus IV without tactile seta; subterminal tarsal setae arcuate and acute; claws of legs unmodified.

Abdomen: Most tergites and sternites with medial suture. Male tergites without lateral keels. Males without paired sac-like invaginations on anterior margins of sternites; males with patches of glandular setae on sternites V–IX, V–VIII, V–X, VII–VIII or IV–IX, females with glandular setae on segments V–IX or VI–X; glandular setae short and conical. Spiracular helix present. Pleural membrane longitudinally striate and somewhat wrinkled.

Genitalia: Male: lateral apodemes extending laterally, with obvious dorsal branches forming chitinized arch; rams horn organs absent; lateral apodemes paired, extending posteriorly. Female: with 1 pair of small lateral cribriform plates and 1 large, median cribriform plate; with a pair of distinct spermathecae.

Remarks.—Species of *Nannowithius* are unusual amongst the Withiidae, as they lack a tactile seta on tarsi III and IV. The only other withiids that lack this seta are *Plesiowithius dekeyersi* and *Termitowithius kistneri*, the sole representatives of *Plesiowithius* and *Termitowithius*, respectively (Vachon 1954; Muchmore 1990). All other withiids possess a tactile seta in the medial or distal section of the tarsus. Eyes are lacking in both species of *Plesiowithius* and *Termitowithius*, and in the majority of *Nannowithius* species; a single pair of eye-spots or corneate eyes is present in all other withiids. The only exceptions appear to be *N. aethiopicus* and *N. paradoxus* (Mahnert, 1980) which are described as having rudimentary eye-spots (Mahnert 1980, 1988).

Vachon (1954) distinguished *Plesiowithius* from *Nannowithius* by the presence of multiple setal rows on the tergites (compared with a single row in *Nannowithius*), and the slightly larger size (e.g., pedipalpal femur 0.93 mm in length, compared with 0.41–0.64 mm in *Nannowithius*). He also listed the presence of glandular setae on sternites V–IX in *Plesiowithius*, but the type species of *Nannowithius*, *N. aethiopicus*, only has glandular setae on sternites VI and VII (Mahnert 1988), and the other species have them on sternites V–IX [*N. buettikeri* (Mahnert, 1980) and *N. pakistanicus* (Beier, 1978)], IV–IX (*N. paradoxus*), IV–VIII (*N. wahrmani*) or V–VII (*N. caecus*, see below). Therefore, the main criteria used by Vachon (1954) to separate *Plesiowithius* from *Nannowithius* no longer apply, and *Plesiowithius* is relegated to the synonymy of *Nannowithius*. Incidentally, four of the five species of *Nannowithius* were originally placed in the aptly named *Myrmecowithius*, which was synonymized with *Nannowithius* by Mahnert (1988).

With the inclusion of *P. dekeyersi* and *W. caecus* in *Nannowithius* (see below), the distribution of the genus now extends from Pakistan through the Middle East to eastern and northern Africa (Fig. 1).

Nannowithius aethiopicus (Simon, 1900)

Chelifer aethiopicus Simon 1900:596.

Type specimens.—ERITREA: *Gash-Barka*: lectotype male, Agordat [15°33′N, 37°53′E], 1896, F. Derchi (MCSNG, not examined). Paralectotype: 1 specimen, collected with lectotype (MNHN, no. 20732) (not examined).

Description.—See Mahnert (1988).

Remarks.—*Nannowithius aethiopicus* is only known from the type locality in Eritrea.

Nannowithius buettikeri (Mahnert, 1980)

Myrmecowithius buettikeri Mahnert 1980:40–42, figs 23–28.

Type specimens.—SAUDI ARABIA: *Ar Riyād*: holotype male, Khushūm al Buwaybīyah (as Kushm al Buwaybiyat) [25°10′N, 46°52′E] (NMB, not examined). Paratypes (NMB,

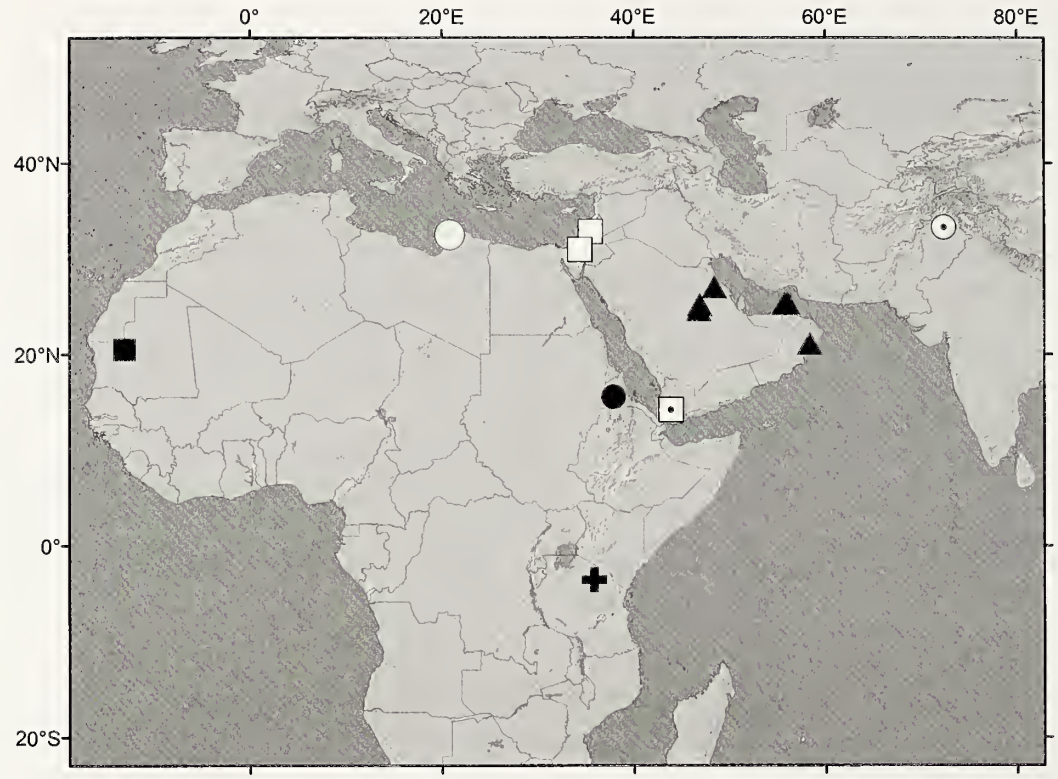


Figure 1.—Map showing distribution of species of the *Nannowithius* group: Nannowithius *aethiopicus* (●); *N. buettikeri* (▲); *N. caecus* (○); *N. dekeyseri* (■); *N. pakistanicus* (⊙); *N. paradoxus* (⊡); *N. wahrmani* (□); *Termitowithius kistneri* (+).

MNHG, not examined): 3 females, collected with holotype; 1 female, Al Khubra [27°01′N, 48°24′E], 29 May 1978, W. Büttiker; 1 female, Riyadh [27°01′N, 48°24′E], 3 March 1978, A. M. Talhouk.

Description.—See Mahnert (1980).

Remarks.—*Nannowithius buettikeri* is known from Saudi Arabia (Mahnert 1980), Oman (Mahnert 1991) and the United Arab Emirates (Mahnert 2009).

Nannowithius caecus (Beier, 1929), comb. nov.
Figs. 2, 3

Withius caecus Beier 1929:78–79, figs 1a–b.

Material examined.—LIBYA: *Banghazi:* holotype male, Marj (as El Merg) [32°29′N, 20°50′E], Cyrenaica, 14 April (year not stated), F. Silvestri (MZUN).

Diagnosis.—*Nannowithius caecus* differs from *N. aethiopicus* and *N. paradoxus* by the lack of eyes or eye-spots, from *N. buettikeri* by the less sharply defined pedicel on the pedipalpal femur, from *N. wahrmani* by the longer chelal fingers, and from *N. dekeyseri* and *N. pakistanicus* by the position of trichobothrium *est* which is situated only slightly distal to *ist* (*est* strongly distal to *ist* in *N. dekeyseri*, and basal to *ist* in *N. pakistanicus*).

Description.—*Adult male:* color: with sclerotized portions generally pale red-brown, legs and sternites paler than remainder of body.

Chelicera: With 5 setae on hand, all acuminate; movable finger with 1 subdistal seta; galea small, with 1–2 small terminal rami; rallum of 4 blades; serrula exterior with 20 blades; lamina exterior present.

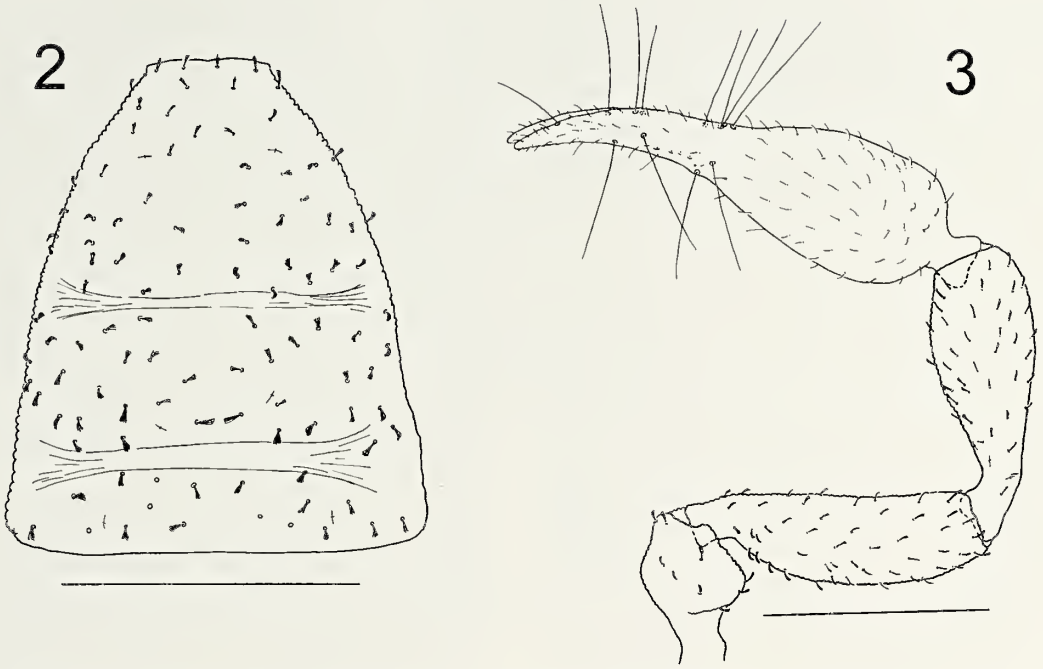
Pedipalp: Trochanter, femur and patella granulate, chela smooth; trochanter 1.76, femur 3.52, patella 2.80, chela (with pedicel) 3.51, chela (without pedicel) 3.24, hand 1.54 x longer than broad, movable finger 1.14 x longer than hand (without pedicel). Femur of male with basal region not expanded (Fig. 3). Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Fig. 3): *eb*, *esb*, *ib* and *ist* situated basally; *isb* and *it* situated sub-medially; *b* and *sb* situated sub-basally near one another; *st* much closer to *t* than to *sb*. Venom apparatus not visible.

Carapace (Fig. 2): 1.18 x longer than broad; posteriorly widened; eyes absent; with 99 setae, including 4 near anterior margin, 42 additional setae in anterior zone, 37 in medial zone and 16 in posterior zone; with 2 distinct furrows; posterior furrow slightly closer to posterior carapaceal margin than to median furrow.

Coxal region: Maxilla with 2 apical setae and 1 very small internal, sub-oral seta, maxilla without rugose area; chaetotaxy of coxae I–IV: 7: 7: 9: 16.

Legs: Junction between femora and patellae I and II only slightly oblique; posterior tarsi without tactile seta; subterminal tarsal setae arcuate and acute; arolium slightly longer than claws.

Abdomen: Tergites and sternites with faint medial suture. Tergal chaetotaxy: 14: 13: 13: 19: 19: 22: 21: 22: 20: 20: 8: 2; mostly uniseriate but some tergites with a few setae placed anteriorly; all setae strongly foliate. Sternal chaetotaxy: 12: (3) 8 (3): (2) 10 (2): 17 + 10/11 gls: 17 + 7/8 gls: 16 + 6/6 gls: 14 + 3/3 gls: 14: 14: 8: 2; sternites V–VII of ♂ with patches of glandular setae; setae uniseriate and acuminate; glandular setae of ♂ stout and conical; ♂ without paired invaginations on anterior margins of sternites.



Figures 2–3.—*Nannowithius caecus* (Beier), holotype male: 2. Carapace, dorsal; 3. Right pedipalp, dorsal. Scale lines = 0.5 mm.

Genitalia: Male with lateral apodemes short, other details not visible in specimens.

Dimensions (mm): Male holotype: Body length 1.94. Pedipalps: trochanter 0.413/0.234, femur 0.686/0.195, patella 0.642/0.229, chela (with pedicel) 1.056/0.301, chela (without pedicel) 0.976, hand length 0.464, movable finger length 0.531. Carapace 0.832/0.706.

Remarks.—Beier (1929) described *Withius caecus* from a single male collected at El Merg, Cyrenaica. This locality is nowadays known as Barce and located in the Libyan district of Benghazi. Beier's choice of name reflected the lack of eyes in the holotype, and he also clearly stated that the posterior tarsi lacks a tactile seta. As all other species currently attributed to *Withius* have eyes which are either rounded, corneate eyes or flat eye-spots, and have a tactile seta on the posterior tarsi, the position of *W. caecus* seems anomalous. The holotype male of *W. caecus* is in good condition and clearly does not belong to *Withius*, and is readily identified as a species of *Nannowithius* by the lack of a tactile seta, the position of the chelal trichobothria and the lack of eyes (Mahnert 1988). Therefore, *W. caecus* is here transferred to *Nannowithius*.

Nannowithius dekeyseri (Vachon, 1954), comb. nov.
Figs. 4–10

Plesiowithius dekeyseri Vachon 1954:1026–1029, figs 6–11.

Material examined.—Syntypes: MAURITANIA: *Adrar*: 1 male, Atar [20°31′N, 13°03′W], May 1949, A. Villiers (MNHN; 3 slides); 1 male, same locality, 26 November 1951, P. Dekeyser and A. Villiers (MNHN; 1 slide consisting only of chelicerae).

Diagnosis.—*Nannowithius dekeyseri* differs from all other species of the genus by the position of trichobothrium *est* which is situated distal to *ist*, but is either basal to *ist* or is opposite *ist* in the other species (Beier 1963, 1978; Mahnert 1980, 1988).

Description.—*Adult male:* color: pedipalps, legs and carapace deep red-brown, other body portions yellow-brown.

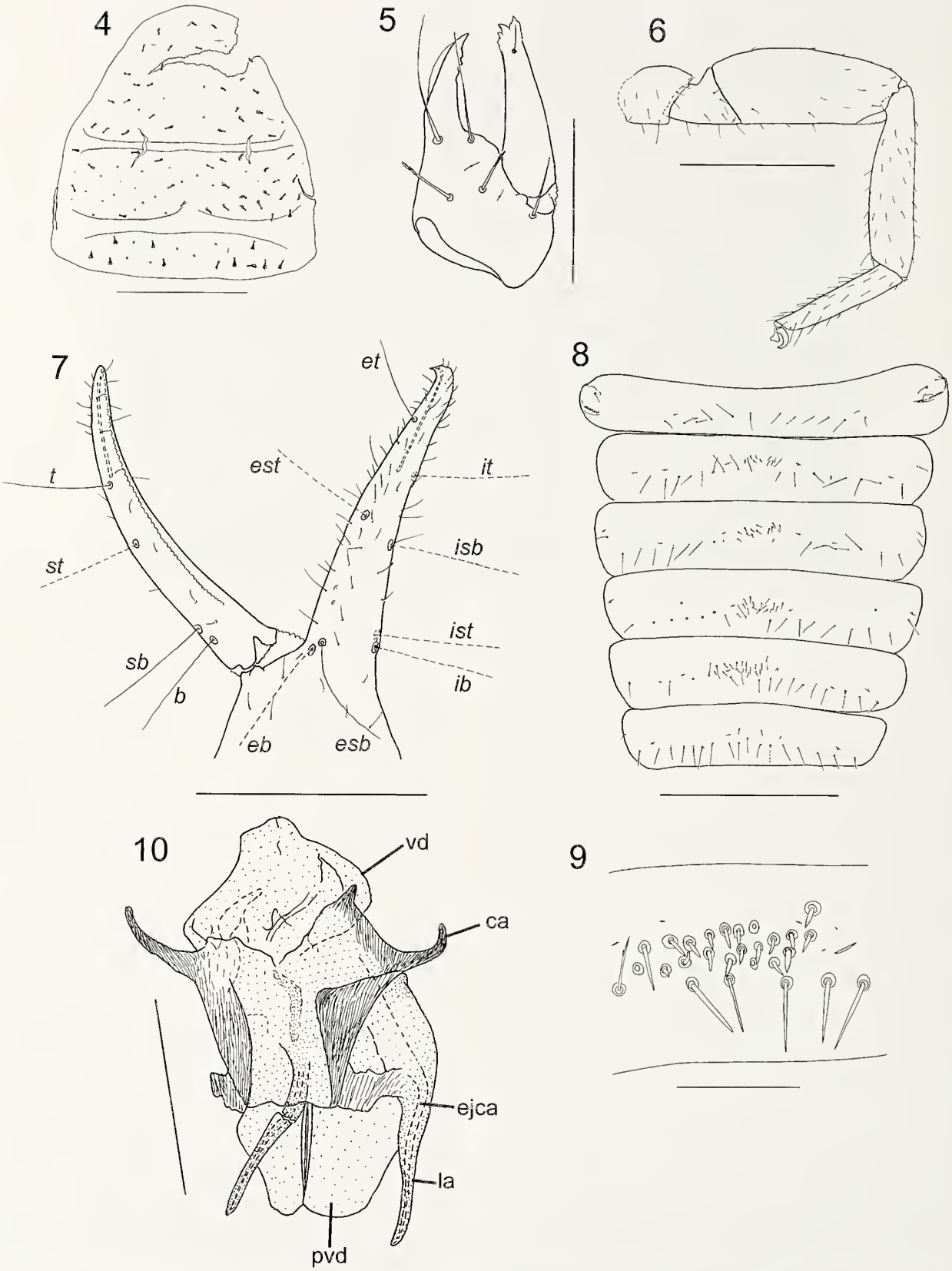
Chelicera (Fig. 5): With 5 setae on hand, *bs* and *sbs* dentate, all others acuminate; movable finger with 1 subdistal seta; galea with 2 small terminal rami; rallum of 4 blades; serrula exterior with 18 blades; lamina exterior present.

Pedipalp: Trochanter, femur and patella coarsely granulate, chela slightly granulate, and fingers smooth; setae generally clavate and denticulate; femur 3.89 x longer than broad. Femur of male with basal region not expanded. Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Fig. 7): *eb*, *esb*, *ib* and *ist* situated basally; *est* and *isb* sub-medial, with *est* situated slightly distal to *isb*; *it* situated sub-distally; *b* and *sb* situated sub-basally near one another; *st* closer to *t* than to *sb*. Venom apparatus present in both chelal fingers, venom ducts long, terminating in nodus ramosus between near *it* in fixed finger and near *t* in movable finger. Retrolateral margin of fixed finger with 2 sense-spots, prolateral margin with 14 sense-spots; retrolateral margin of movable finger with 2 sense-spots, prolateral margin with 3 sense-spots. Chelal teeth small; fixed finger with 46 teeth; movable finger with 48 teeth; accessory teeth absent.

Carapace (Fig. 4): ca. 1.05 x longer than broad; posteriorly widened; eyes absent; with 97 strongly foliate setae, including 32 in anterior zone, 48 in medial zone and 17 in posterior zone; with 2 distinct furrows; posterior furrow slightly closer to posterior carapaceal margin than to median furrow.

Coxal region: Maxilla with 2 apical setae and 1 very small internal, sub-oral seta, plus 16 additional setae, maxilla without rugose area; chaetotaxy of coxae I–IV: 9: 8: 9: ca. 20.

Legs: Junction between femora and patellae I and II slightly oblique to long axis; junction between femora and patellae III and IV very angulate; femora III and IV much smaller than patellae III and IV (Fig. 6); femur + patella of leg IV 3.12 x longer than broad; tarsi III and IV without tactile seta;



Figures 4–10.—*Nannowithius dekeyersi* (Vachon), syntype male: 4. Carapace, dorsal; 5. Left chela, lateral; 6. Right chelicera; 7. Left leg IV; 8. Sternites IV–IX, ventral; 9. Sternite VIII, detail of setae; 10. Genitalia, ventral. Scale lines = 0.5 mm (Figs. 4, 5, 7, 8), 0.2 mm (Figs. 6, 9, 10).

subterminal tarsal setae arcuate and acute; claws of legs unmodified; arolium shorter than claws (Fig. 6).

Abdomen: Tergites I–X with suture line; sternites V–VII with faint medial suture. Tergal chaetotaxy: 15: 15: 13: 16: 20: 19: 20: 23: 21: 20: 16: 2; tergites I–III and X uniseriate, IV uniseriate but with pair of discal setae, and V–IX biseriate; all setae strongly foliate. Sternal chaetotaxy: 15: (2) 10 (2): (2) 13 [0+0] (2): 19 + 12 gls: 21 + 17 gls: 18 + 15 gls: 15 + 21 gls: 20 + 2 gls: 11: 12: 2; sternites V–VIII of ♂ with patches of glandular setae (Fig. 9); sternites V–VI uniseriate but with pair of discal setae, and VIII–X uniseriate; glandular setae of ♂ stout and conical; ♂ without paired invaginations on anterior margins of sternites.

Genitalia (Fig. 10): Lateral apodemes extending laterally, with obvious dorsal branches forming chitinized arch; rams horn organs absent; lateral apodemes paired, extending posteriorly.

Dimensions (mm): Male syntype: body length ca. 2.9. Pedipalps: not measurable. Chelicera 0.272/0.170, movable finger length 0.207. Carapace ca. 1.06/1.008. Leg I: femur 0.187/0.195, patella 0.429/0.169, tibia 0.461/0.129, tarsus 0.378/0.080. Leg IV: femur + patella 0.755/0.242, tibia 0.619/0.142, tarsus 0.435/0.088.

Remarks.—Vachon (1954) described this species from two males collected in north-western Mauritania. One of these males, collected during March 1949, is mounted on three mieroscope slides and in fair condition. The chelae are crushed and immeasurable, and the carapace is slightly flattened and cracked (Fig. 4). The other specimen, collected during September 1951, is only represented by the chelicerae, which are also slide-mounted.

Nannowithius pakistanicus (Beier, 1978)

Myrmecowithius pakistanicus Beier 1978:233–234, fig 2.

Type specimens.—PAKISTAN: *Punjab*: holotype male, Kohala, Kashmir [33°17′N, 72°22′E], 3,000 feet, in nest von *Messor* sp., 13 June 1974, C. Baroni Urbani (NMB, not examined). Paratypes: 3 males, collected with holotype (NMB, NHMW, not examined)

Description.—See Beier (1978).

Remarks.—*Nannowithius pakistanicus* is only known from the type locality in Pakistan.

Nannowithius paradoxus (Mahnert, 1980)

Myrmecowithius paradoxus Mahnert 1980:38–40, figs 17–22.

Type specimens.—YEMEN: *Ibb*: holotype male, Wadi Zabib [14°11′N, 43°53′E], November 1971, A. Szalai-Marzso (HNHM, not examined). Paratype: 1 female, collected with holotype (MNHG, not examined).

Description.—See Mahnert (1980).

Remarks.—*Nannowithius paradoxus* is only known from the type locality in Yemen.

Nannowithius wahrmani (Beier, 1963)

Myrmecowithius wahrmani Beier 1963:196–197, fig 8

Type specimens.—Syntypes: ISRAEL: *HaDarom (Southern)*: 3 males, 1 female, 2 tritonymphs, Wadi Abyad [30°57′N, 34°23′E], aus einem Nest van *Messor semirufus*, 27 March 1952, J. Wahrman (HUJ, not examined).

Description.—See (Beier 1963). Mahnert (1975) provided an illustration of the female genitalia.

Remarks.—*Nannowithius wahrmani* is only known from the type locality, Wadi Abyad Beier (1963) and Mt. Arbel (Mahnert 1974), both located in Israel.

Genus *Termitowithius* Muchmore, 1990

Termitowithius Muchmore 1990:125.

Type species.—*Termitowithius kistneri* Muchmore, 1990, by original designation.

Diagnosis.—*Termitowithius* is the only withiid genus that lacks a fully developed venom apparatus in the chelal fingers (Figs. 17, 18). It also is the only genus that lacks abdominal glandular setae that also lacks a tactile seta on tarsi III and IV (Fig. 21).

Description.—*Adults:* Chelicera (Fig. 12): with 5 setae on hand and 1 subdistal seta on movable finger; seta *bs* and *sbs* dentate, remaining setae acuminate; seta *bs* and *sbs* much shorter than others; rallum of 4 blades, the most distal blade with several serrations on leading edge, other blades smooth (Fig. 13).

Pedipalp (Figs. 15, 16): Chelal fingers greatly elongated, movable finger much longer than hand (without pedicel). Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Fig. 16): *est* situated closer to *et* than to *esb*; *it* situated subdistally; *st* situated closer to *t* than to *sb*; *sb* situated much closer to *b* than to *st*. Retrolateral margin of chelal fingers with numerous sensilla, more numerous on fixed chelal finger. Venom apparatus absent in both chelal fingers, nodus ramosus absent.

Carapace (Fig. 11): Eyes absent; with 2 furrows, posterior furrow situated closer to posterior carapace margin than to anterior furrow.

Legs (Figs. 20. 21): Junction between femora and patellae I and II slightly oblique to long axis; tarsus IV without tactile seta; subterminal tarsal setae arcuate and acute; claws of legs unmodified.

Abdomen: Male tergites without lateral keels; all setae thickened and strongly dentate (Fig. 22); glandular setae absent.

Genitalia: Male (Fig. 24): lateral apodemes extending laterally, with obvious dorsal branches forming chitinized arch; rams horn organs absent; lateral apodemes paired, extending posteriorly, very slender. Female (Fig. 25): with 1 pair of small lateral cribriform plates and 1 large, median cribriform plate with small protrusions; spermathecae not visible.

Remarks.—Muchmore (1990) suggested that *Termitowithius* should be included in the Withiidae, despite the lack of glandular setae on the sternites, a feature that is found in most other withiids apart from *Protowithius* Beier, 1955 from Juan Fernandez Islands and *Juxtachelifer* Hoff, 1956 from southwestern U.S.A. (Beier 1955b; Hoff 1956; Harvey 1992b). He reasoned that the morphology of the anterior pairs of legs in which the junction between the femora and patellae was perpendicular or only slightly oblique was characteristic of all Withiidae, including *Termitowithius*.

The affinities of *Termitowithius* within the family Withiidae are difficult to discern. While it resembles *Protowithius* and *Juxtachelifer* in the lack of glandular setae on the sternites, it

seems to be most similar to *Nannowithius* which is the only other withiid that lack a tactile seta on tarsi III and IV, and which lack eyes or have the eyes reduced to rudimentary eye-spots. All other withiids have a strongly developed tarsal tactile setae, and eyes in the form of distinct eye-spots or rounded, corneate eyes.

Termitowithius kistneri Muchmore, 1990
Figs. 11–25

Termitowithius kistneri Muchmore 1990:126–127, figs 1–7.

Material examined.—TANZANIA: *Arusha*: holotype male, Lake Manyara National Park [3°35′S, 35°50′E], from fungus gardens in nest (T–374) of *Macrotermes subhyalinus* (Blattodea: Termitidae), 19 June 1970, D.H. Kistner (FSCA WM2662.01001). Paratypes: TANZANIA: Arusha: 1 female (allotype), collected with holotype (FSCA WM2662.01003); 1 male, 1 female, collected with holotype (FSCA WM2662.01002, 4).

Diagnosis.—As for genus.

Description.—*Adults:* color: sclerotized portions generally light red-brown, coxae and legs lighter. Pedipalps, carapace, and to a lesser extent, tergites and legs, with an obvious pseudoderm layer.

Chelicera (Fig. 12): With 5 setae on hand and 1 subdistal seta on movable finger; seta *bs* and *sbs* dentate, remaining setae acuminate; seta *bs* and *sbs* much shorter than others; with 2 dorsal lyrifissures and 1 ventral lyrifissure; galea of ♂ and ♀ with ca. 10 small terminal rami (Fig. 14); rallum of 4 blades, the most distal blade with several serrations on leading edge, other blades smooth (Fig. 13); serrula exterior 19 (♂, ♀) blades; lamina exterior present.

Pedipalp (Fig. 15): Surfaces of trochanter, femur and patella granulate, chela smooth; patella with 2 small sub-basal lyrifissures; trochanter 1.62–1.76 (♂), 1.58–1.64 (♀), femur 3.86–4.30 (♂), 4.00–4.18 (♀), patella 3.53–3.88 (♂), 3.45–3.50 (♀), chela (with pedicel) 6.11–6.24 (♂), 5.68–5.88 (♀), chela (without pedicel) 5.91–5.96 (♂), 5.46–5.69 (♀), hand 2.17 (♂), 2.02 (♀) x longer than broad, movable finger much longer than hand (without pedicel), 1.74–1.76 (♂), 1.74–1.85 (♀) x longer than hand (without pedicel). Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Fig. 16): *eb* and *esb* situated basally, *ib* and *ist* subbasally, *est* and *isb* submedially, *et* and *it* subdistally, *est* situated distal to *isb*; *t* situated subdistally, *st* slightly closer to *t* than *sb*, and *sb* situated much closer to *b* than to *st*. Diploid sensillum situated slightly basal to *st*. Venom apparatus absent from both chelal fingers, but vestigial venom ducts present in distal tooth (Figs. 17, 18). Retrolateral margin of chelal fingers with numerous sensilla, more numerous on fixed chelal finger. Chelal teeth rounded; fixed finger with 48 (♂, ♀) teeth; movable finger with 52 (♂, ♀) teeth; accessory teeth absent.

Carapace (Fig. 11): Coarsely granulate; 0.89–0.95 (♂), 0.99–1.01 (♀) x longer than broad; eyes absent; with ca. 169 (♂), 181 (♀) setae, arranged with ca. 68 (♂), 70 (♀) (including 4 (♂), 5 (♀) near anterior margin) in anterior zone, ca. 65 (♂), 70 (♀) in median zone, and ca. 36 (♂), 41 (♀) in posterior zone; with few lyrifissures; with 2 furrows, posterior furrow situated closer to posterior carapace margin than to anterior furrow; posterior margin with median indentation.

Coxal region: Maxillae lightly granulate near anterior and lateral margins, remainder smooth; coxae smooth; manducatory process with 2 apical and subapical acuminate setae, plus 1 small sub-oral seta, and 21 (♂), 23 (♀) additional setae; median maxillary lyrifissure rounded and situated submedially; posterior maxillary lyrifissure rounded. Coxa IV of male not modified; coxal sac absent. Chaetotaxy of coxae I–IV: ♂, 10: 14: 14: 22; ♀, 10: 17: 19: 24.

Legs (Figs. 20, 21): Junction between femora and patellae I and II slightly oblique to long axis; junction between femora and patellae III and IV very angulate; femora III and IV much smaller than patellae III and IV; femur + patella of leg IV 2.90–3.13 (♂), 2.92–3.06 (♀) x longer than broad; tarsi III and IV without tactile seta; subterminal tarsal setae arcuate and acute; claws of legs unmodified; arolium shorter than claws.

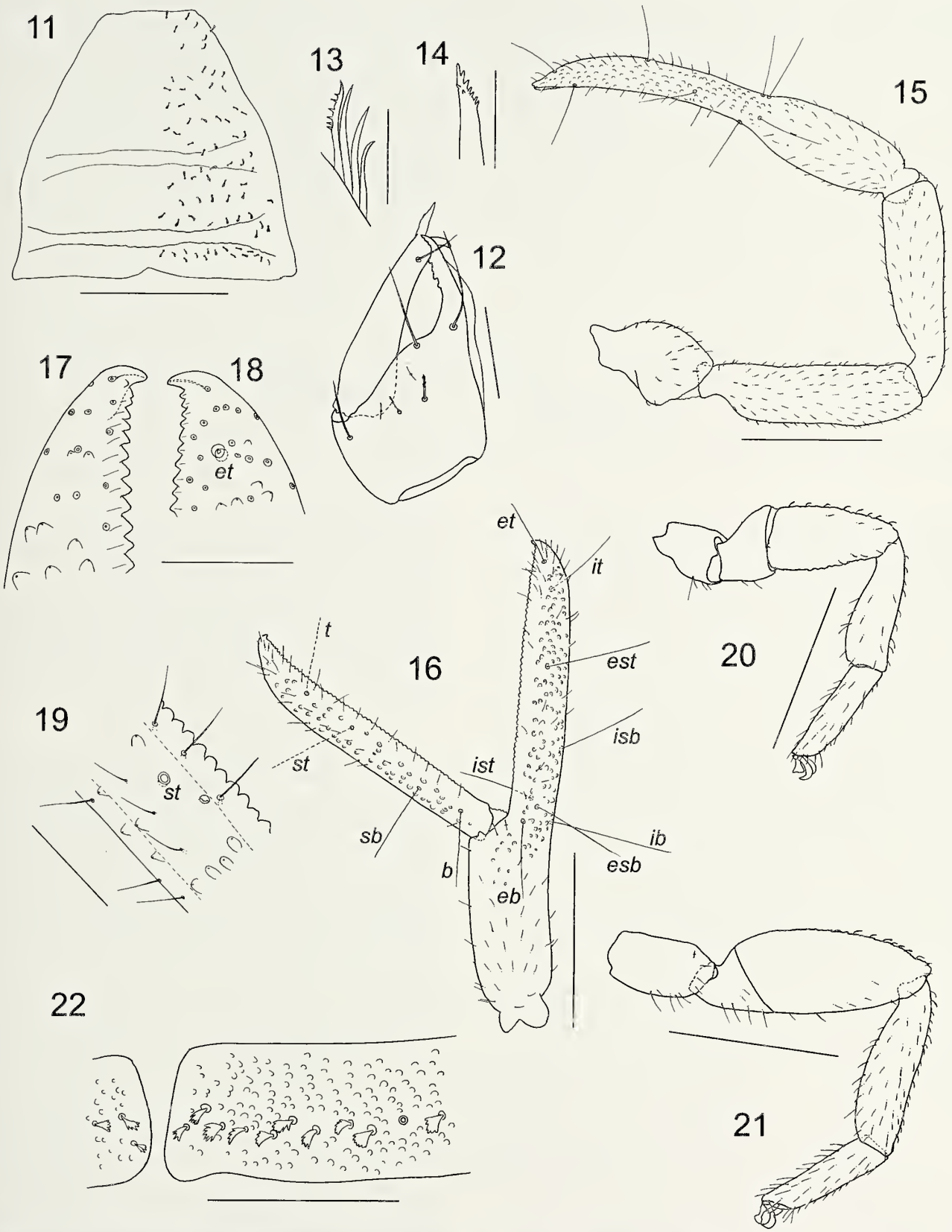
Abdomen: Tergites I–X and sternites V–X with median suture line (Fig. 22). Tergal chaetotaxy: ♂, 35: 35: 41: 43: 46: 44: 46: 46: 49: 41: 30: 2; ♀, 44: 43: 45: 49: 53: 50: 59: 55: 55: 49: 25: 2; tergites irregularly uniseriate except for multiple discal seta on the posterior tergites; all setae thickened and strongly dentate (Fig. 22); ♂ tergites without lateral keels. Sternal chaetotaxy: ♂, 19: (1) 15 [0+0] (1): (1) 16 (1): 21: 20: 21: 20: 21: 19: 14: 2; ♀, 19: (1) 22 (2): (1) 18 (1): 23: 24: 24: 21: 20: 15: 12: 2; sternites irregularly uniseriate, except for lateral discal seta on sternites IX–XI; all setae acicular; ♂ sternite II with scattered setae (Fig. 23); glandular setae absent. Spiracles with helix. Anal plates (tergite XII and sternite XII) situated between tergite XI and sternite XI. Pleural membrane finely wrinkled-plicate; without any setae.

Genitalia: Male (Fig. 24): lateral apodemes extending laterally, with obvious dorsal branches forming chitinized arch; rams horn organs absent; lateral apodemes paired, extending posteriorly, very slender. Female (Fig. 25): with 1 pair of small lateral cribriform plates and 1 large, median cribriform plate with small protrusions; spermathecae not visible.

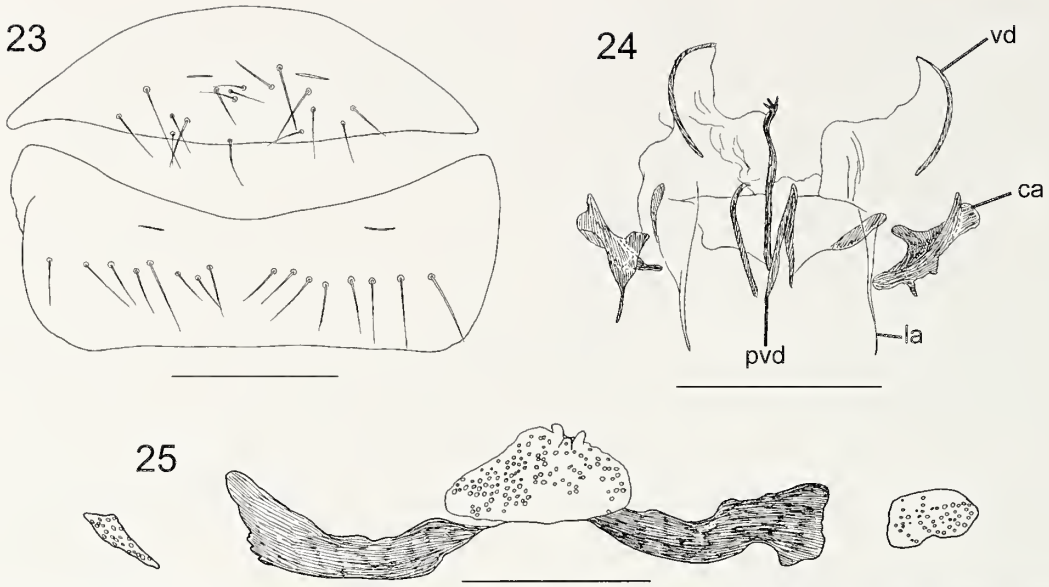
Dimensions (mm): Male holotype followed by male paratype (where applicable): Body length 2.45 (2.79). Pedipalps: trochanter 0.445/0.275 (0.475/0.27), femur 0.81/0.21 (0.86/0.20), patella 0.76/0.215 (0.795/0.205), chela (with pedicel) 1.405/0.23 (1.435/0.23), chela (without pedicel) 1.36 (1.37), hand length 0.50 (0.50), movable finger length 0.87 (0.88). Chelicera 0.29/0.165, movable finger length 0.22. Carapace 0.91/1.025 (0.89/0.94). Leg I: femur 0.18/0.18, patella 0.375/0.185, tibia 0.40/0.13, tarsus 0.35/0.09. Leg IV: femur + patella 0.695/0.24 (0.72/0.23), tibia 0.535/0.145, tarsus 0.38/0.095.

Female allotype followed by female paratype (where applicable): Body length 3.54 (3.38). Pedipalps: trochanter 0.46/0.29 (0.46/0.28), femur 0.84/0.21 (0.835/0.20), patella 0.76/022 (0.77/0.22), chela (with pedicel) 1.42/0.25 (1.41/0.24), chela (without pedicel) 1.365 (1.365), hand length 0.505 (0.485), movable finger length 0.88 (0.895). Chelicera 0.29/0.17, movable finger length 0.19. Carapace 0.985/0.975 (0.97/0.975). Leg I: femur 0.20/0.175, patella 0.41/0.185, tibia 0.405/0.135, tarsus 0.355/0.075. Leg IV: femur + patella 0.745/0.255 (0.735/0.24), tibia 0.55/0.145, tarsus 0.41/0.10.

Remarks.—Muchmore (1990) examined 11 adult specimens, of which the four slide-mounted specimens (the holotype, allotype and two paratypes) were examined for this study.



Figures 11–22.—*Termitowithius kistneri* Muchmore, holotype male, unless stated otherwise: 11. Carapace, dorsal; 12. Left chelicera; 13. Right rallum, female allotype; 14. Galea; 15. Right pedipalp, dorsal; 16. Left chela, lateral; 17. Tip of chelal finger; 18. Tip of movable chelal finger; 19. Teeth of movable chelal finger; 20. Leg I; 21. Leg IV; 22. Right tergite III. Scale lines = 0.5 mm (Figs. 11, 15, 16, 20, 21), 0.2 mm (Fig. 22), 0.1 mm (Figs. 12, 17–19), 0.05 mm (Figs. 13, 14).



Figures 23–25.—*Termitowithius kistneri* Muchmore: 23. Genital sternites, male paratype; 24. Genitalia, ventral, male paratype; 25. Genitalia, female allotype. Scale lines = 0.2 mm (Figs. 23, 24), 0.1 mm (Fig. 25).

As explained by Muchmore (1990), *Termitowithius kistneri* is a highly modified inquiline that is found within the fungus gardens in the nests of the African termite *Macrotermes subhyalinus* (Rambur, 1842). The fungus gardens of macrotermitine nests are composed of the fungus *Termitomyces* which is cultivated by the termites, presumably to provide nutrition through the breakdown of grasses brought into the nest by the termites. The apparent modifications for an inquiline existence of *T. kistneri* include the lack of eyes, and the highly modified chelae of the pedipalps. The chelal fingers are greatly enlarged, and are nearly twice as long as the chelal hand (Fig. 16), and the retrolateral margins of the fingers bear numerous sensilla that are more numerous on the fixed finger (Fig. 16). The venom apparatus of *T. kistneri* appears to be completely absent, as the venom tooth of both fingers is reduced in size, and the venom duct is restricted to a small channel within the venom tooth (Figs. 17, 18), but does not lead into a long venom duct and associated nodus ramosus found with the chelal fingers of all other species assigned to the suborder Iocheirata (e.g. Chamberlin 1931; Harvey 1992b; Murienne et al. 2008). It is not known whether the pseudoscorpion feeds on termites or some other inquiline in the nest, but it seems apparent that they have foregone using venom to subdue their prey and instead use their massive chelal fingers to grasp and probably crush their prey.

The termite host *Macrotermes subhyalinus* is widely distributed across much of tropical Africa (Ruelle 1970), where they build mounds with extensive subterranean galleries (Tilahun et al. 2012).

BIOLOGY

Some species of the genus *Nannowithius* and *Termitowithius kistneri*, which are the only withiids that lack a tactile seta on the posterior tarsi (see above), have strong affinities with social insects (Table 1). The original specimens of *N. wahrmanni* were collected from a nest of the ant *Messor semirufus* (André, 1883) in southern Israel (Beier 1963), whereas other specimens were found under stones but with no recorded association with ants (Mahnert 1974). Specimens of *N. pakistanicus* were also found

Table 1.—Locality and habitat data for species of *Nannowithius* and *Termitowithius*.

Species	Locality	Habitat	Reference
Nannowithius aethiopicus	ERITREA: Agordat	not stated	Simon (1900)
Nannowithius buettikeri	SAUDI ARABIA: Khushūm al Buwaybīyah; Al Khubra; Riyadh	not stated	Mahnert (1980)
	OMAN: Shaqq	not stated	Mahnert (1991)
	UNITED ARAB EMIRATES: Sharjah Desert Park	light trap	Mahnert (2009)
	UNITED ARAB EMIRATES: Wadi Maidaq	in leaf litter	Mahnert (2009)
Nannowithius caecus	LIBYA: Barce	not stated	Beier (1929)
Nannowithius dekeyseri	MAURITANIA: Atar	not stated	Vachon (1954)
Nannowithius pakistanicus	PAKISTAN: Kohala	in nest of *Messor* sp.	Beier (1978)
Nannowithius paradoxus	YEMEN: Wadi Zabib	not stated	Mahnert (1980)
Nannowithius wahrmani	ISRAEL: Wadi Abyad	in nest of *Messor semirufus*	Beier (1963)
	ISRAEL: Mt Arbel	under stones	Mahnert (1974)
Termitowithius kistneri	TANZANIA: Lake Manyara National Park	from fungus gardens in nest of *Macrotermes subhyalinus*	Muchmore (1990)

in the nests of ants (*Messor* sp.) (Beier 1978), and although the original description of *N. buettikeri* (Mahnert, 1980) contained no mention of habitat data (Mahnert 1980), specimens collected a few years later were recovered from light traps and leaf litter (Mahnert 2009), with at least the light trap records suggesting they were attached to flying insects. The termitophile *T. kistneri* has only been collected from the nest of the termite *Macrotermes subhyalinus* (Muchmore 1990). All other collections of the remaining four species of *Nannowithius*, *N. aethiopicus*, *N. caecus*, *N. dekeyseri* and *N. paradoxus*, lack any mention of habitat data (Table 1). While the evidence is not particularly overwhelming, it is likely that all species of these two withiid genera are associated with social insects, *Nannowithius* with ants and *Termitowithius* with termites. Further evidence of an obligate existence with social insects may lie with the lack of eyes in *Termitowithius* and in most species of *Nannowithius*. Only *N. aethiopicus* and *N. paradoxus* have eye-spots which are reported to be rudimentary (Mahnert 1980, 1988).

The only other withiids that are known to be associated with social insects are *Girardwithius pumilus* Heurtault, 1994 and *Rexwithius girardi* Heurtault, 1994 which occur in the defunct galleries of *Macrotermes* termites in west Africa (Heurtault 1994). The presence of tarsal setae in both species (Heurtault 1994) does not suggest a particularly close relationship with either *Nannowithius* or *Termitowithius*.

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Revised diagnoses for the pseudoscorpion genera *Metawithius* and *Microwithius*, with the description of a new Australian genus, and notes on *Withius* (Pseudoscorpiones, Withiidae)

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Abstract. Pseudoscorpions of the family Withiidae are distributed in most regions of the world, but are less common in the Australian region. Apart from the cosmopolitan genus *Withius* Kew, 1911, the fauna is dominated by the endemic genera *Metawithius* Chamberlin, 1931 and *Hyperwithius* Beier, 1951. A review of material of both genera reveals that *Metawithius* is a senior synonym of *Hyperwithius*, and is defined by the presence of a patch of rugose cuticle on the internal surface of the male maxilla. The genus contains the following taxa: *M. murrayi* (Pocock, 1900), *M. philippinus* Beier, 1937, *M. spiniventer* Redikorzev, 1938, *M. spiniventer pauper* Beier, 1953, three species newly transferred from *Hyperwithius* to *Metawithius*, *M. annamensis* (Redikorzev, 1938), comb. nov., *M. tonkinensis* (Beier, 1951), comb. nov. and *M. dawydoffi* (Beier, 1951), comb. nov., and *M. nepalensis* (Beier, 1974) which is newly transferred from *Withius*. The remaining species previously attributed to *Metawithius* are transferred to other genera, primarily because they lack the patch of rugose cuticle. The subgenus *Metawithius (Microwithius)* Redikorzev, 1938 is once again raised to generic level, and provisionally contains four species, *M. yurii* Redikorzev, 1938 from southeast Asia, and *M. indicus* (Murthy and Ananthakrishnan, 1977), comb. nov., *M. chamundiensis* (Sivaraman, 1980), comb. nov. and *M. bulli* (Sivaraman, 1980), comb. nov. from India. *Metawithius (Microwithius) tweediei* Beier, 1955 also lacks the rugose patch of cuticle and is provisionally transferred to *Withius*, forming the new combination *W. tweediei* (Beier, 1955). Two new species from northern Australian rainforests are found to be most similar to *Metawithius* but instead of an internal patch of rugose cuticle, they have an external patch. These new species, *R. bulbosus* sp. nov. (type species) and *R. longissimus* sp. nov., are placed in a new genus, *Rugowithius*. *Afrowithius* Chamberlin, 1931 is regarded as a new synonym of *Withius*, and the type species *Chelifer paradoxus* Ellingsen, 1912 from South Africa is treated as a senior synonym of *Withius crassipes* (Lawrence, 1937).

Keywords: Taxonomy, new species, morphology, new synonyms

Pseudoscorpions of the family Withiidae occur in many parts of the world, but are most abundant in tropical and sub-tropical biotopes. Species of *Withius* Kew, 1911 are found all over the world, and *Sphaerowithius* Mahnert, 1988 is found in Africa and the Solomon Islands but the sole Solomon Islands species, *S. salomonensis* (Beier, 1966), is morphologically somewhat anomalous and its relationship with other members of the genus requires further testing (Mahnert 1988). The remaining 34 withiid genera show strong biogeographic fidelity with 21 genera restricted to the sub-Saharan region of Africa (including various peripheral islands such as Ascension, Reunion, Mauritius, Seychelles and Saint Helena) and the adjacent Middle East, eight genera restricted to the Ameriean region (ranging from southern U.S.A. to the Archipiélago Juan Fernández), and two genera endemic to southeastern Asia, *Metawithius* Chamberlin, 1931 and *Hyperwithius* Beier, 1951 (Harvey 2013). The sole fossil genus, *Beierowithius* Mahnert, 1979 with one included species *B. sieboldtii* (Menge, 1854), has been found in Tertiary Baltic Amber deposits, but appears to differ little from Recent taxa based on the available descriptions (Menge, in Koch & Berendt 1854; Menge 1855; Beier 1937b, 1955a).

Metawithius currently contains nine species which are distributed throughout the Asian region from India to the Indonesian archipelago (Harvey 2013). It is divided into two subgenera, *M. (Metawithius)* and *M. (Microwithius)* Redikorzev, 1938, although the latter was initially described as a distinct genus (Redikorzev 1938) before being treated as a subgenus by Beier (1951). The status of the three species of *Hyperwithius*, which were originally based upon small differences in pedipalp proportions, abdominal setation and the shape of the male coxa IV (Beier 1951), was questioned by Schawaller (1995).

The discovery of two new species of Withiidae in northern Australia has prompted a reexamination of the status of *Metawithius* and *Hyperwithius*, and the subgenus *Microwithius*. While the Australian species were found to resemble *Metawithius* and *Hyperwithius* in some morphological features, they were found to differ in others and are here placed in a new genus which is named *Rugowithius*. In addition to treating *Hyperwithius* as a junior synonym of *Metawithius*, the subgenus *Microwithius* is once again treated as a valid genus. One of the species previously included in *Microwithius*, *Me. (Mi.) tweediei* Beier, 1955, is tentatively transferred to *Withius* as it lacks the morphological features of both *Metawithius* and *Microwithius*. To aid future research into this group, the type species of *Metawithius*, *M. murrayi* (Pocock, 1900), is redescribed based on the type specimens and other material. And finally, the status of the African genus *Afrowithius* Chamberlin, 1931, is examined and shown to be based on an anomalous specimen; the genus is synonymized with Withius.

METHODS

The specimens used for this study are lodged in the following institutions: Natural History Museum, London (BMNH); Museum and Art Gallery of the Northern Territory Museum, Darwin (MAGNT): Muséum d'Histoire Naturelle, Geneva (MHNG); Naturhistorisches Museum, Basel (NHMB); Naturhistorisches Museum, Wien (NHMW); Museum Victoria, Melbourne (NMV); Queensland Museum, Brisbane (QM); Senckenberg Gesellschaft für Naturforschung, Frankfurt am Main (SMF); Western Australian Museum, Perth (WAM); and Zoological Museum, University of Copenhagen (ZMUC).

The specimens were examined by preparing a temporary slide mount by immersing the specimen in 75% lactic acid at room temperature for several days, and mounting them on microscope slides with 10 mm coverslips supported by small sections of 0.25 mm diameter nylon fishing line. The specimens were observed with an Olympus BH-2 or a Leica DM2500 compound microscope and illustrated with the aid of a drawing tube. Measurements were taken at the highest possible magnification using an ocular graticule. After study, the specimens were rinsed in water and returned to 75% ethanol with the dissected portions placed in 12 x 3 mm glass genitalia microvials (BioQuip Products, Inc.). The scanning electron micrographs were obtained in a Philips XL30 scanning electron microscope after the specimens were prepared by dehydration in 1,1,1,3,3,3–Hexmethyldisilazane (HMDS), air-dried and mounted on SEM stubs with carbon tape.

Terminology and mensuration mostly follow Chamberlin (1931a), with the exception of the nomenclature of the pedipalps and legs, and with some minor modifications to the terminology of the trichobothria (Harvey 1992), cheliceral setation (Harvey & Edward 2007), cheliceral rallum (Judson 2007) and faces of the appendages (Harvey et al. 2012). The synonymies under each taxon only include the original description; subsequent descriptions and generic transfers may be found in Harvey (2013). The ratio TS is the distance from the base of tarsus IV to the tactile seta, divided by the length of the entire tarsus. The abbreviation gls refers to the abdominal glandular setae found on the sternites of many withiids. The following abbreviations are used for the male genitalia: ca, chitinized arch; dd, dorsal diverticulum; ejca, ejaculatory canal atrium; la, lateral apodeme; md, median diverticulum.

SYSTEMATICS

Family Withiidae Chamberlin, 1931

Male genitalic morphology.—The male genitalia of some withiids are modified such that the lateral apodemes are long, somewhat triangular and bear an extended ejaculatory canal that extends posteriorly far into the abdomen. This state has been found in a variety of both Old World and New World withiid genera including some species of *Withius* [including *W. hispanus* (L. Koch, 1873), *W. faunus* (Simon, 1879), *W. neglectus* (Simon, 1878) (Heurtault 1971; pers. obs.) and *W. japonicus* Morikawa, 1954 (Morikawa 1954)], *Balanowithius* Beier, 1959 (pers. obs.), *Cacodemonius* Chamberlin, 1923 (Chamberlin 1923; pers. obs.), *Cystowithius* Harvey, 2004 (Harvey 2004), *Dolichowithius* Beier, 1932 (pers. obs.), *Metawithius* (pers. obs.), *Microwithius* (Harvey 1988), *Parawithius* Beier, 1932 (Harvey 2004), *Pycnowithius* Beier, 1979 (Mahnert 1988), *Rexwithius* Heurtault, 1994 (Heurtault 1994), *Rugowithius* gen. nov. (pers. obs.), *Thaumatowithius* Beier, 1940 (pers. obs.), *Trichotowithius* Beier, 1944 (Dashdamirov 1992) and *Victorwithius* Beier, 1932 (pers. obs.). Other withiids possess shortened lateral apodemes that look more similar to the configuration found in other cheliferoids. These include many species of *Withius* including the type species *W. piger* (Simon, 1879) (e.g., Chamberlin 1931a; Beier 1947; Heurtault 1971; Mahnert 1988), *Aisthetowithius* Beier, 1967 (Mahnert 1988), *Cryptowithius* Beier, 1967 (pers. obs.), *Girardwithius* Heurtault, 1994 (Heurtault 1994), *Ectromachernes* Beier, 1944 (Vachon 1952), *Juxtachelifer* Hoff, 1956 (pers. obs.), *Nannowithius* Beier, 1932 (Mahnert 1988; Harvey in press), *Stenowithius* Beier, 1932 (Mahnert 1988; pers. obs.), *Nesowithius* Beier, 1940 (pers. obs.), *Parallowithius* Beier, 1955 (pers. obs.), *Pogonowithius* Beier, 1979 (pers. obs.), *Scotowithius* Beier, 1977 (pers. obs.), *Sphallowithius* Beier, 1977 (pers. obs.), *Stenowithius* Beier, 1932 and *Termitowithius* Muchmore, 1990 (pers. obs.). The triangular conformation is rather striking, and would appear to signify that this group of genera represent a monophyletic group which is here termed the *Cacodemonius* group. There is an available genus-group name, the Cacodemoniini Chamberlin, 1931 (Chamberlin 1931b), which can be used for this group. The remaining genera are not supported by any known synapomorphy, and changes to the subfamily or tribal classification are not proposed until a robust phylogenetic analysis can be performed.

The male genitalic morphology confirms that at least four species currently included in *Withius* are misplaced and should be removed to another genus. These four species, *W. hispanus*, *W. faunus*, *W. neglectus* and *W. japonicus*, are unlikely to be the only misplaced species, as many species of *Withius* lack descriptions or illustrations of the male genitalia and the number of misplaced species will most likely increase. In addition, the internal trichobothrial series of the chelal fingers of these four species as well as *Withius despaxi* Vachon, 1937 are all basally clustered with trichobothria *it* and *isb* situated virtually adjacent to each other (Beier 1932a; Vachon 1937; Morikawa 1954), unlike most other species of *Withius* in which the trichobothria are slightly more widespread with *it* and *isb* separated from each other (e.g., Beier 1932a; Mahnert 1988).

Genus *Metawithius* Chamberlin, 1931

Metawithius Chamberlin 1931b:293.
Hyperwithius Beier 1951:99–100. **Syn. nov.**

Type species.—*Metawithius: Chelifer murrayi* Pocock, 1900, by original designation.

Hyperwithius: Sundowithius annamensis Redikorzev, 1938, by original designation.

Diagnosis.—Species of *Metawithius* differ from all other genera of Withiidae in the possession of a small patch of rugose cuticle on the internal surface of the maxilla of males, which is situated slightly anterior to the median maxillary lyrifissure (Fig. 5); the only other pseudoscorpion with a similar feature is *Rugowithius*, in which this patch is situated externally on the maxilla (Fig. 17). Males also differ from other withiids by the sub-oral setae of maxilla being on a 'hooked' mound (Fig. 5). It further differs from *Rugowithius* by the sternal glandular setae of males being short and conical (Fig. 11)

(long and distally spatulate in *Rugowithius*), the glandular setae of males being present on sternites IV–X, and occasionally XI (on sternites VI–IX in *Rugowithius*) (Fig. 10) and the spermathecal reeeptacula of females coiled (not coiled in *Rugowithius*) (Fig. 13).

Description.—Setae: most dorsal setae strongly elavate and denticulate; setae on sternites acicular.

Chelicera (Fig. 2): With 5 setae on hand, *sbs* always denticulate, *bs* either denticulate or acuminate, *es*, *ls* and *is* always acuminate; movable finger with 1 subdistal seta (*gs*); rallum of 4 blades (Fig. 3), the most distal blade with several serrations on leading edge, other blades smooth; lamina exterior present.

Pedipalp: Not particularly sexually dimorphic; femur of male without hypertrophied base (Fig. 4). Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Fig. 7); trichobothria *ib*, *ist*, *isb* and *it* grouped in basal half of finger. Venom apparatus present in both chelal fingers, venom ducts long, terminating in nodus ramosus slightly basal to *et* in fixed finger and distal to *t* in movable finger. Chelal teeth all closely spaced; accessory teeth absent.

Carapace: With 2 non-corneate eyes; with 2 furrows, anterior furrow distinct, posterior furrow indistinct; posterior furrow closer to posterior margin of carapace than to anterior furrow.

Coxal region: Median maxillary lyrifissure present and submedially situated (Figs. 5, 6); sub-oral seta of male maxilla on 'hooked' mound (Fig. 5); males with patch of ridged cuticle on internal margin of maxilla (Fig. 5).

Legs: Junction between femora and patellae I and II only slightly oblique; tactile seta of posterior legs sub-medial (Fig. 1); subterminal tarsal setae arcuate and acute; arolium slightly shorter than claws; claws slender and simple.

Abdomen: Most tergites and sternites with medial suture. Male tergites without lateral keels. Males without paired sac-like invaginations on anterior margins of sternites; males with patches of glandular setae on most sternites (Fig. 10), females with 2 glandular setae on segments VIII–IX; glandular setae of male short and conical (Fig. 11). Spiracular helix present. Pleural membrane longitudinally striate and somewhat wrinkled.

Genitalia: Male genitalia with long, triangular lateral apodemes (Fig. 12); female genitalia with T-shaped spermathecae, each receptaculum coiled (Fig. 13).

Remarks.—All of the males included in the genus *Metawithius* examined during this study were found to possess a small internal patch of rugose cuticle situated near the midline of the maxilla (Fig. 5). This feature has not been detected in any other withiid examined to date. It was first noticed and illustrated by With (1906, plate III fig. 8g) but has apparently gone unnoticed since, even by the normally attentive J.C. Chamberlin when he created the genus *Metawithius* (Chamberlin 1931b). The function of this bizarre structure remains to be discovered and its presence only in adult males hints at some sort of sexual function such as a pheromone-producing or receiving region. This conjecture is reinforced by the presence of parallel ridges on the structure that may serve to increase the surface area of the organ. The other feature shared by species of *Metawithius* is the excavated mesal margin of the male maxilla such that the sub-oral seta is borne on a small protuberance (Fig. 5).

These two features are found in the type species of *Metawithius*, *M. murrayi*, as well as males of *M. philippinus, M. spiniventer*, *Hyperwithius dawydoffi* Beier, 1951, *H. tonkinensis* Beier, 1951 and *Withius nepalensis* Beier, 1974, which calls into question the status of the genus *Hyperwithius*. This genus was originally distinguished from *Metawithius* by the proximally widened pedipalpal femur. Although specimens of the type species of *Hyperwithius*, *Sundowithius annamensis* Redikorzev, 1938, were not examined for this study, there is little doubt that they will have all the morphological features mentioned above. The only appreciable differences between species of *Metawithius* and *Hyperwithius* appear to be the shape of the pedipalpal femur which in species of *Hyperwithius* possess a slightly expanded basal region which is lacking in *Metawithius*. This difference is not considered sufficient to warrant the retention of separate genera and the genus *Hyperwithius* is relegated as a junior synonym of *Metawithius*, and reflects the comments of Heurtault (1986) who suggested that *Hyperwithius* should be regarded as a subgenus of *Metawithius*.

Metawithius includes seven species and one subspecies, *M. annamensis* (Redikorzev, 1938), *M. dawydoffi* (Beier, 1951), *M. murrayi* (Pocock, 1900), *M. nepalensis* (Beier, 1974), *M. philippinus* Beier, 1937, *M. spiniventer* Redikorzev, 1938, *M. spiniventer pauper* Beier, 1953 and *M. tonkinensis* (Beier, 1951). The other species that have been previously attributed to *Metawithius* are treated below under the genus *Microwithius* and the genus *Withius*.

Metawithius murrayi (Pocock, 1900)
Figs. 1–13

Chelifer murrayi Pocock 1900: 156–157, plate 16 fig. 1, 1a.

Material examined.—*Lectotype.* AUSTRALIA: *Christmas Island:* male, North West Point [10°26'S, 105°33'E], August 1897, C.W. Andrews (BMNH 1898.10.14.8).

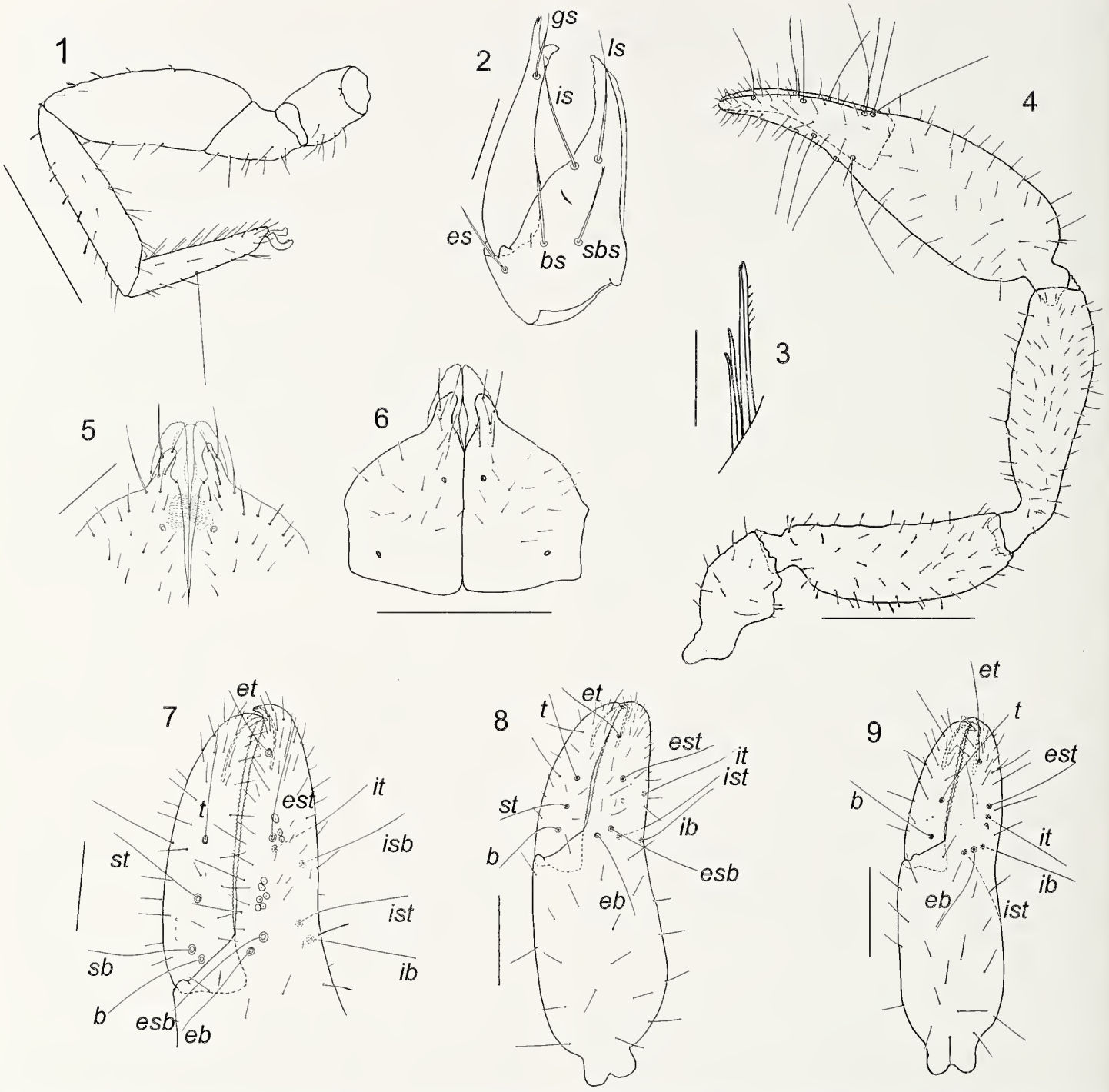
Paralectotype. 1 female, same data as lecotype (BMNH 1898.10.14.9).

Other material: AUSTRALIA: *Christmas Island:* 1 tritonymph, below Tom's Ridge Road, 1 km E. of West White Beach walking track, site 7E, 10°30'S, 105°40'E, 18 June 1990, primary rainforest, P. Green (WAM T110459). INDIA: *Andaman and Nicobar Islands*: Nicobar Islands: 1 male, Nankovry [7°59'N, 93°32'E], Galatea Expedition (ZMUC, no. 23); 1 male, 1 female, Car Nikobar [9°10'N, 92°47'E], Galatea [Expedition] (ZMUC, no. 25). INDONESIA: *Nusa Tenggara:* 1 male, 1 female, 1 deutonymph, Sui, Timor, 9°50'S, 124°29'E, 14 August 1990, D. Agosti (WAM T78680); 1 female, same data (WAM T78681); *Sumatera Barat*: 1 male, 1 tritonymph, Lac Maninjau (36 km de Bukittinggi), Lawang, à env. 5 km de Maninjau, au bord du lac, 0°20'S, 100°11'E, 21 July 1984, J. Robert (MHNG). MYANMAR: *Mandalay*: 4 males, 1 female, Maymyo [22°02'N, 96°28'E], 700–800 m, sous écorce, 12 February 1996, S. Kurbatov (MHNG).

Diagnosis.—*Metawithius murrayi* appears to be most similar to *M. philippinus* but differs in the reduced number of glandular setae on the male sternites.

Description.—*Adults:* Colour: with sclerotized portions generally dark red-brown; carapaceal metazone without paired pale spots.

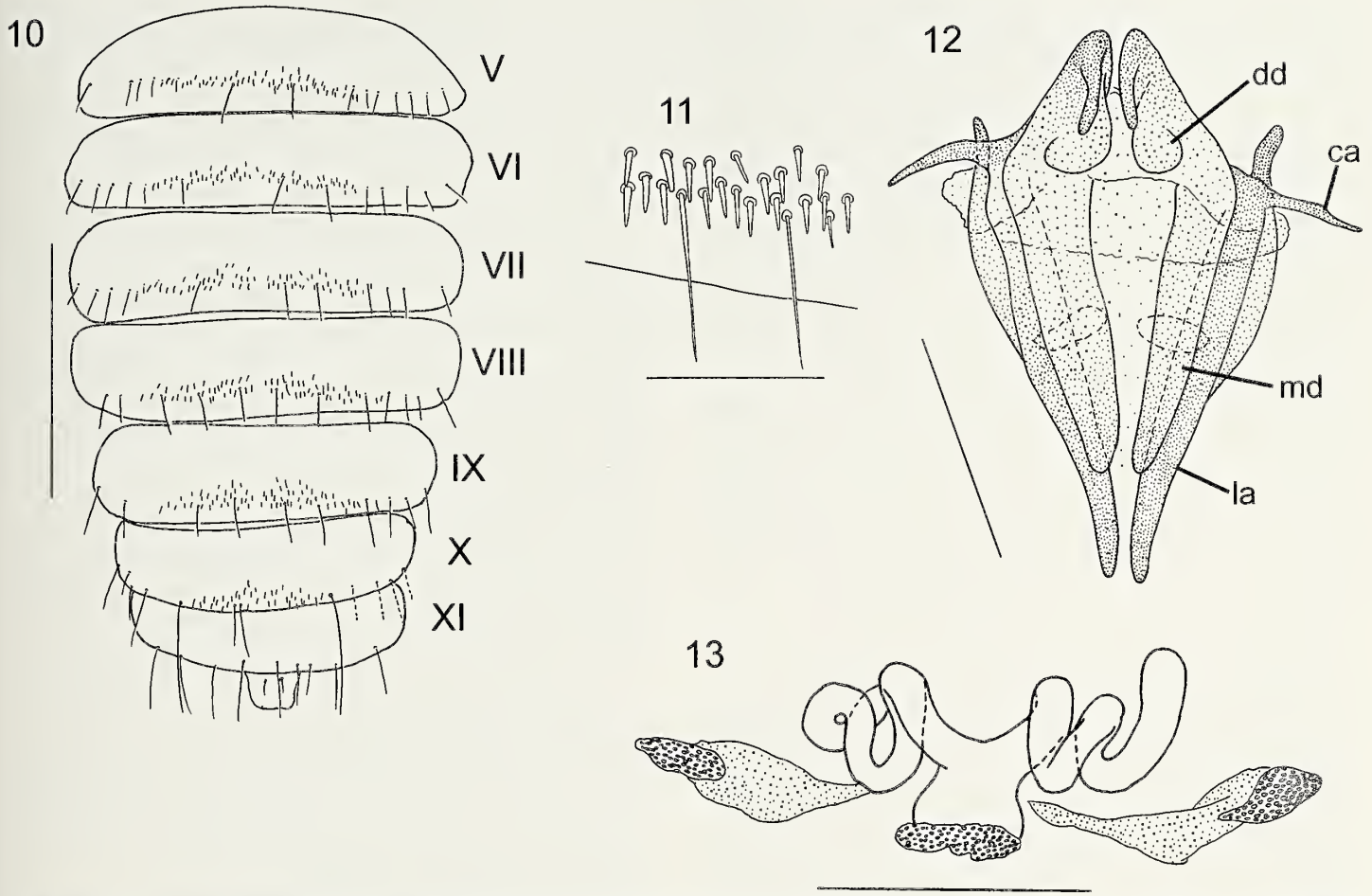
Chelicera (Fig. 2): With 5 setae on hand, *sbs* slightly dentate, *bs* smooth; movable finger with 1 subdistal seta; galea of male with 3 very small terminal rami, of female with 1 sub-terminal



Figures 1–9.—*Metawithius murrayi* (Pocock): 1. Left leg IV, male from Timor (WAM T78680); 2. Left chelicera; 3. Rallum, male from Timor (WAM T78680); 4. Right pedipalp, dorsal, lectotype male; 5. Maxillae, male from Timor (WAM T78680); 6. Maxillae, female from Timor (WAM T78680); 7. Left chela, male from Timor (WAM T78680); 8. Left chela, tritonymph from Lac Maninjau Sumatera Berat (MHNG); 9. Left chela, deutonymph from Timor (WAM T78680). Scale lines = 0.5 mm (Figures 1, 4–6); 0.2 mm (Figures 7–9); 0.1 mm (Figure 2); 0.05 mm (Figure 3).

and 4 terminal rami; rallum of 4 blades, the most distal blade with several serrations on leading edge, other blades smooth (Fig. 3); serrula exterior with 20 (♂), 18 (♀) blades; lamina exterior present.

Pedipalp: Trochanter, femur and patella granulate, chela smooth; dorsal setae clavate and denticulate; trochanter 1.88 (♂), 1.84 (♀), femur 3.25 (♂), 3.24 (♀), patella 3.53 (♂), 2.99 (♀), chela (with pedicel) 3.57 (♂), 3.17 (♀), chela (without pedicel) 3.35 (♂), 3.00 (♀), hand 1.97 (♂), 1.86 (♀) x longer than broad, movable finger 0.74 (♂), 0.69 (♀) x longer than hand. Femur of male with basal region not expanded (Fig. 4). Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Fig. 7): *eb* and *esb* situated basally; trichobothria *ib*, *ist*, *isb* and *it* grouped in basal half of finger; *b* and *sb* situated near one another; *st* slightly closer to *sb* than to *t*. Venom apparatus present in both chelal fingers, venom ducts



Figures 10–13.—*Metawithius murrayi* (Pocock), lectotype male unless stated otherwise: 10. Abdominal segments V–XII, ventral; 11. Glandular setae, sternite VII, left hemi-sternite; 12. Male genitalia, ventral, male from Timor (WAM T78680); 13. *Metawithius* sp. from Maymyo, Myanmar (MHNG), female, genitalia, ventral. Scale lines = 0.5 mm (Figure 10); 0.2 mm (Figures 12, 13); 0.1 mm (Figure 11).

long, terminating in nodus ramosus slightly basal to *et* in fixed finger and distal to *t* in movable finger. External margin of fixed finger with 6 sense-spots situated midway between *esb* and *est*, and with 3 near *est*; external margin of movable finger with three sense-spots situated between *sb* and *st*, within a common sulcus. Chelal teeth rounded; fixed finger with 37 (♂), 41 (♀) teeth; movable finger with 42 (♂), 45 (♀) teeth; accessory teeth absent.

Carapace: 1.24 (♂), 1.23 (♀) x longer than broad; lateral margins strongly convex, not posteriorly widened; with 2 non-corneate eyes; with ca. 71 (♂), 78 (♀) setae, including 4 (♂, ♀) near anterior margin and 9 (♂), 8 (♀) near posterior margin; with 2 furrows, with distinct anterior furrow and indistinct posterior furrow; posterior furrow slightly closer to posterior carapaceal margin than to median furrow.

Coxal region: Coxal chaetotaxy: ♂, 12: 10: 12: 23, ♀, 12: 12: 10: 25; maxilla with 2 apical setae and 1 very small internal, sub-oral seta (Figs. 5, 6); interno-median region of male maxilla with rugose area; sub-oral seta of male maxilla on 'hooked' mound (Fig. 5).

Legs: Junction between femora and patellae I and II only slightly oblique; femur + patella of leg IV 2.70 (♂), 2.66 (♀) x longer than broad; tarsal tactile seta of leg IV situated medially, 0.46 (♂), 0.51 (♀) of tarsus length (Fig. 1); subterminal tarsal setae arcuate and acute; arolium slightly shorter than claws.

Abdomen: Tergites and sternites with faint medial suture. Tergal chaetotaxy: male, 8: 9: 10: 10: 12: 12: 13: 12: 12: 11: 12 (including 4 tactile setae): 2; ♀, 11: 12: 13: 15: 15: 16: 16: 18: 15: 14: 10 (including 2 tactile setae): 2; mostly uniseriate but some tergites with a few setae placed anteriorly; all setae foliate. Sternal chaetotaxy: male, 13: (2) 10 (2): (2) 8 + gls 1/0 (2): 14 + 29/22 gls: 16 + 26/24 gls: 11 + 30/32 gls: 13 + 35/29 gls: 11 + 34/29 gls: 12 (including 2 tactile setae) + 17/18 gls: 13 (including 4 tactile setae): 2; ♀, 12: (3) 9 (3): (2) 11 (2): 18: 20: 20: 17 + 1/1 gls: 14 + 1/1 gls: 9 (including 2 tactile setae): 12 (including 4 tactile setae): 2; sternites IV–X of male with patches of glandular setae (Fig. 10); glandular setae ca. 26 μm in length, stout and conical (Fig. 11); sternites VIII–IX of female with glandular setae; setae uniseriate and acuminate; male without paired invaginations on anterior margins of sternites.

Genitalia: Male with elongated and posteriorly tapering lateral apodemes (Fig. 12); female with 2 tubes each with approximately two coils (Fig. 13), with a single median cribriform plate and a pair of lateral cribriform plates, and with triangular, sclerotised lateral apodemes (Fig. 13).

Dimensions (mm): Males: lectotype, followed by other males (where applicable): body length 2.65. Pedipalps: trochanter 0.48/0.255, femur 0.86/0.265 (0.724–0.976/0.251–0.266), patella 0.935/0.265 (0.792–1.056/0.259–0.269), chela (with pedicel) 1.32/0.370 (1.107–1.411/0.328–0.410), chela (without pedicel) 1.24 (1.039–1.328), hand length 0.73 (0.776), movable finger length 0.54 (0.560). Chelicera 0.275/0.136, movable finger length 0.202. Carapace 0.872/0.704 (width at medial area); eye diameter 0.076. Leg I: tibia 0.350/0.088, tarsus 0.328/0.060. Leg IV: femur + patella 0.670/0.248, tibia 0.535/0.075, tarsus 0.400/0.071, TS 0.182.

Female: Paralectotype, followed by other males (where applicable): body length 3.07. Pedipalps: trochanter 0.46/0.25, femur 0.825/0.255 (0.95–1.066/0.28–0.313), patella 0.825/0.276 (0.98–1.101/0.30–0.334), chela (with pedicel) 1.33/0.42 (1.54–1.640/0.46–0.531), chela (without pedicel) 1.26 (1.48–1.557), hand length 0.78 (0.86–0.928), movable finger length 0.54 (0.66–0.648). Chelicera 0.275/0.136, movable finger length 0.202. Carapace 0.910/0.740 (width at medial area); eye diameter 0.064. Leg I: tibia 0.362/0.090, tarsus 0.336/0.063. Leg IV: femur + patella 0.665/0.250, tibia 0.560/0.121, tarsus 0.390/0.075, TS 0.200.

Tritonymph (from Christmas Island, WAM T110459): Colour: pale yellow-brown, pedipalps red-brown.

Chelicera: With 5 setae on hand and a single seta (*gs*) on movable finger; rallum with 4 blades, the anterior blade with 4 spinules on anterior face, other blades smooth.

Pedipalp: Trochanter 1.85, femur 3.07, patella 2.95, chela (with pedicel) 3.56, chela (without pedicel) 3.36, hand 1.87 x longer than broad. Fixed chelal finger with 7 trichobothria, movable chelal finger with 3 trichobothria (Fig. 8): *isb* and *sb* absent.

Carapace: 1.24 x longer than broad; with 2 non-corneate eyes; with ca. 60 setae, including 5 near anterior margin and 6 near posterior margin; with deep median furrow and shallow posterior furrow.

Coxal region: Maxilla with 2 apical setae and 1 very small internal, sub-oral seta; internal margin of pedipalpal coxa unmodifed.

Legs: TS = 0.48.

Abdomen: Tergal chaetotaxy: 6: 7: 7: 10: 10: 10: 10: 10: 8: 10: 6 (arranged T4T): 2. Sternal chaetotaxy: 4: (1) 6 (1): (1) 6 (1): 11: 10: 9: 9 + 1/1 gls: 9 + 1/1 gls: 8 (arranged 2T2T2): 6 (arranged 1T2T1): 2; sternites VII–VIII each with 2 glandular setae.

Dimensions (mm): Body length 1.78. Pedipalps: trochanter 0.336/0.182, femur 0.590/0.192, patella 0.598/0.203, chela (with pedicel) 0.965/0.271, chela (without pedicel) 0.911, hand length 0.508, movable finger length 0.390. Carapace 0.699/0.563.

Deutonymph (from Timor, WAM T78680): Colour: pale yellow-brown, with pedipalps and carapace red-brown.

Chelicera: With 5 setae on hand and a single seta (*gs*) on movable finger; rallum with 4 blades, the anterior blade with 4 spinules on anterior face, other blades smooth.

Pedipalp: Trochanter 1.89, femur 3.14, patella 2.82, chela (with pedicel) 3.49, chela (without pedicel) 3.26, hand 1.87 x longer than broad. Fixed chelal finger with 6 trichobothria, movable chelal finger with 2 trichobothria (Fig. 9): *esb*, *isb* and *sb* and *st* absent.

Carapace: 1.42 x longer than broad; with 2 non-corneate eyes; with ca. 31 setae, including 4 near anterior margin and 6 near posterior margin; with 2 furrows, a shallow anterior furrow and a deep posterior furrow.

Coxal region: Maxilla with 2 apical setae and 1 very small internal, sub-oral seta; internal margin of pedipalpal coxa unmodifed.

Legs: TS = 0.47.

Abdomen: Tergal chaetotaxy: 6: 6: 6: 6: 6: 6: 6: 6: 6: 6: 6: 8 (arranged T1T2T1T): 2. Sternal chaetotaxy: 0: (0) 4 (0): (2) 4 (2): 6: 6: 6: 6 + 1/1 gls: 6 + 1/1 gls: 8 (arranged 2T2T2): 8 (arranged 2T2T2): 2; sternites VIII–IX each with 2 glandular setae.

Dimensions (mm): Body length 1.80. Pedipalps: trochanter 0.280/0.148, femur 0.461/0.147, patella 0.451/0.160, chela (with pedicel) 0.760/0.218, chela (without pedicel) 0.710, hand length 0.408, movable finger length 0.336. Carapace 0.664/0.468.

Remarks.—The syntype specimens of *M. murrayi* are in good condition and although the label reads "1898.10.14.7–9", possibly implying that the vial contained three specimens, only two specimens are included (Judson 1997, and pers. obs.). The male is here nominated as the lectotype. *Metawithius murrayi* occurs throughout southeast Asia, including Christmas Island, Nicobar Islands, Myanmar, Sumatra and Timor.

Metawithius annamensis (Redikorzev, 1938), comb. nov.

Sundowithius annamensis Redikorzev 1938:101–103, figs. 29–31.

Type material.—*Holotype.* VIETNAM: *Quảng Nam*: male, Mount Ba Na (as Bana), near Da Nang (Tourane) [16°04'N, 108°13'E], 1400 m, 28 September 1931, forêt tropicale, C. Dawydoff (MNHN, not examined).

Remarks.—Redikorzev (1938) described this species from a single male collected in Vietnam, but no other specimens have been identified. Although no specimens were examined for this study, the original description by Redikorzev (1938) depicts a withiid with very similar characteristics to *H. dawydoffi* and *H. tonkinensis*, and it is clear that it is a species of *Metawithius*.

Metawithius dawydoffi (Beier, 1951), comb. nov.
Fig. 14

Hyperwithius dawydoffi Beier 1951: 102–104, figs. 34a, 35.

Material examined.—*Syntypes:* **Vietnam:** *Lam Dong*: 4 males, Cao Nguyen Lâm Vien (as Plateau von Langbian) [12°00'N, 108°25'E], 1938–1939, C. Dawydoff (NHMW).

Remarks.—*Hyperwithius dawydoffi* was described from five males from "Plateau von Langbian", Vietnam by Beier (1951), of which four were available for this study. As these males possess all the characteristics of *Metawithius*, including the internal patch of rugose cuticle and pre-oral seta on a hooked mound (Fig. 14), it is transferred to that genus.

Metawithius nepalensis (Beier, 1974), comb. nov.

Withius nepalensis Beier, 1974: 277–278, fig. 11.

Material examined.—*Holotype:* NEPAL: *Central*: Daman, Mahabarat region [27°41'N, 85°07'E], under bark of *Rhododendron arboreum*, February 1970, J. Martens (SMF 28969).

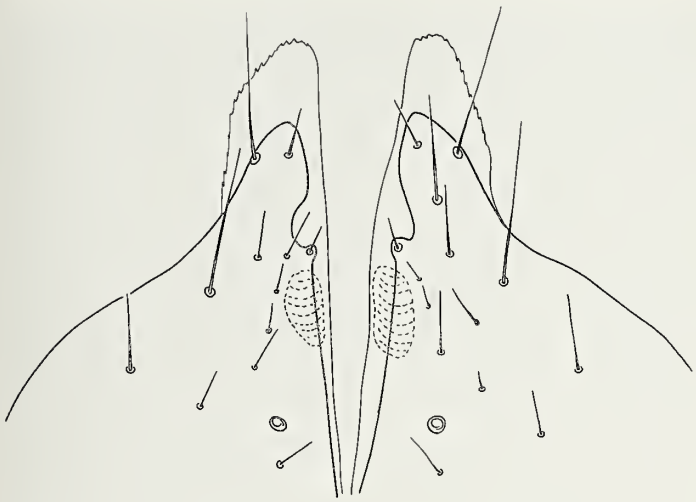


Figure 14.—*Metawithius dawydoffi* (Beier), syntype male, maxillae, ventral. Scale line = 0.2 mm.

Allotype: NEPAL: *Central*: 1 female, collected with holotype (SMF 28970).

Remarks.—The male holotype of *W. nepalensis* from central Nepal has all the characteristics of *Metawithius*, including the internal pateh of rugose cuticle and pre-oral seta on a hooked mound, it is transferred to that genus.

Metawithius philippinus Beier, 1937

Metawithius philippinus Beier 1937:274–275, fig. 5.

Material examined.—*Holotype.* PHILIPPINES: *Bataan*: female, Luzon Island, Limay [14°34'N, 120°36'E], 30 July 1915, S. Böttcher, V. Heyne (ZMB 31879).

Paratypes. PHILIPPINES: *Bataan*: 2 males, 4 females, Luzon Island, Limay [14°34'N, 120°36'E], March 1914, S. Böttcher, V. Heyne (ZMB 31880); *Lanao del Norte:* 3 females, Mindanao Island, Balo-i (as Mommangan) [8°07'N, 124°14'E], 23 February 1915, S. Böttcher, V. Heyne (ZMB 31882); North Luzon Island: *Ilocos Norte*: 2 females, Prov. Bangui [18°28'N, 120°45'E], January 1918, S. Böttcher, V. Heyne (ZMB 31881).

Remarks.—*Metawithius philippinus* was described from the Philippines by Beier (1937a). Males possess all the charaeteristics of *Metawithius*, and it is retained in that genus.

Metawithius spiniventer Redikorzev, 1938

Metawithius spiniventer Redikorzev 1938:103–106, figs. 32–34.

Material examined.—MALAYSIA: *Pahang*: 1 male, Kampung Kuala Terla, Telom Valley, Cameron Highlands [4 32'N, 101 25'E], ca. 4500 feet elevation, March 1935, M.W.F. Tweedie (NHMW). VIETNAM: *Lam Dong:* 3 males, 10 females, 6 nymphs, Cao Nguyen Lâm Vien (as Plateau von Langbian) [12°00'N, 108°25'E], 1938–1939, C. Dawydoff (NHMW).

Remarks.—Redikorzev (1938) described this species from three collections from Vietnam and Cambodia, and further specimens have been reported from Vietnam (Beier 1951, 1967), Malaysia (Beier 1955b) and Thailand (Beier 1967; Schawaller 1994). Males possess all the characteristics of *Metawithius*, and it is retained in that genus.

Metawithius spiniventer pauper Beier, 1953

Metawithius spiniventer pauper Beier 1953:86, fig. 5.

Material examined.—*Syntypes.* INDONESIA: *Nusa Tenggara Timur*: 1 male, 4 females, Langgai, Sumba [10°03'S, 120°27'E], "unter Rinde eines Baum stumpfes beim Seelein Pakaba Mata", 10 July 1949, Bühler, Sutter (NHMB).

Remarks.—Beier (1953a) described *Metawithius spiniventer pauper* from a male and six females from Sumba. The male possess all the characteristics of *Metawithius*, including the internal patches of rugose cuticle on the maxilla, and the taxon is retained in *Metawithius*. Beier (1953a) separated this taxon from the nominate subspecies, *M. spiniventer spiniventer*, by its smaller size. However, its status is uncertain as he did not compare it with other similar taxa, including *M. murrayi* and *M. philippinus*. It was not possible during this study to resolve the status of this taxon, which is here retained as a subspecies of *M. spiniventer* until more detailed work can be undertaken on the species of *Metawithius*.

Metawithius tonkinensis (Beier, 1951), comb. nov.

Hyperwithius tonkinensis Beier 1951:100–102, figs. 33, 34b.

Material examined.—*Syntypes.* VIETNAM: *Lai Chau*: 1 male, 1 female, 2 protonymphs, Lai Chau [22°04'N, 103°10'E], June 1939, C. Dawydoff (NHMW).

Remarks.—The syntypes of *Hyperwithius tonkinensis* have the morphological features found in *Metawithius*, including the internal patches of rugose cuticle on the maxilla. It is therefore transferred to *Metawithius*.

Genus ***Rugowithius*** gen. nov.
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:
BEA73C4B-6AEE-46DC-8387-4A62967CB58E

Type species.—*Rugowithius bulbosus* sp. nov.

Diagnosis.—The genus *Rugowithius* differs from all other withiids by the presence of a small patch of rugose euticle on the external surface slightly posterior to the median maxillary lyrifissure in males (Figs. 16, 17), the bulbous, hypertrophied postero-basal portion of the male pedipalpal femur (Figs. 18, 19, 24, 33), and the expanded tips of the sternal glandular setae (Fig. 21). It strongly resembles *Metawithius* in the presence of a patch of rugose cuticle on the maxilla, but in *Metawithius* the patch is situated internally (Fig. 5). It further differs from *Metawithius* by the glandular setae of males being present on sternites VI–IX (on IV–X, and occasionally XI, in *Metawithius*), and the spermathecal receptacula of females being not coiled (coiled in *Metawithius*) (Fig. 32).

Description.—Setae: most dorsal setae strongly clavate and denticulate; setae on sternites acicular.

Chelicera (Fig. 25): With 5 setae on hand, *bs* and *sbs* slightly denticulate, others acuminate; movable finger with 1 subdistal seta; rallum of 4 blades, the most distal blade with several serrations on leading edge, other blades smooth (Fig. 26); lamina exterior present.

Pedipalps: Sexually dimorphic with that of males longer than females (Figs. 23, 24, 33, 34, 37); femur of male with

hypertrophied base (Figs. 18, 19, 24, 33). Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Figs. 29, 35); trichobothria *ib*, *ist*, *isb* and *it* grouped in basal half of finger. Venom apparatus present in both chelal fingers, venom ducts long, terminating in nodus ramosus slightly basal to *et* in fixed finger and distal to *t* in movable finger. Chelal teeth all closely spaced; accessory teeth absent.

Carapace (Fig. 22): With 2 non-corneate eyes; with 2 furrows, anterior furrow distinct, posterior furrow indistinct; posterior furrow closer to posterior margin of carapace than to anterior furrow.

Coxal region: Median maxillary lyrifissure present and submedially situated; medial margin of maxilla not 'hooked' (Fig. 16); males with medial margin concave and with distinct patch of ridged cuticle on external surface posterior to median maxillary lyrifissure (Fig. 17).

Legs: Junction between femora and patellae I and II only slightly oblique (Fig. 27); tactile seta of posterior legs submedial (Fig. 28); subterminal tarsal setae arcuate and acute; arolium slightly shorter than claws; claws slender and simple.

Abdomen: Tergites I–X with medial suture, sternites VI–IX with faint medial suture. Male tergites without lateral keels. Males without paired sac-like invaginations on anterior margins of sternites; males with patches of glandular setae on sternites VI–IX (Fig. 20), females with 2 glandular setae on segments VIII–IX; glandular setae of male long and distally spatulate (Fig. 21). Spiracular helix present. Pleural membrane longitudinally striate and somewhat wrinkled.

Genitalia: Male with elongated and posteriorly rounded lateral apodemes (Fig. 31); female with T-shaped spermathecae, each receptaculum not coiled (Figs. 32, 36).

Remarks.—*Rugowithius* is the first indigenous withiid genus recorded from mainland Australia, with only the introduced, synanthropic *Withius piger* previously known (Beier 1966b, as *Withius subruber* (Simon)). The genus appears to be restricted to northern Australia where it inhabits tropical forests.

Etymology.—The generic name refers to the corrugated patch of cuticle on the male maxillae (*ruga*, Latin, crease, wrinkle) (Brown 1956) combined with the generic name *Withius* which is derived from the eminent Danish pseudoscorpionologist Carl Johannes With (1877–1923) who first noticed and illustrated the remarkable maxillary feature discussed in this paper. It is masculine in gender.

Rugowithius bulbosus sp. nov.
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:35051601-547A-4EA4-B787-990FF483D3F0
Figs. 15–32

Material examined.—*Holotype.* AUSTRALIA: *Northern Territory:* holotype male, Manngarre Rainforest, Cahills Crossing, banks of East Alligator River, Kakadu National Park, 12°25'30"S, 132°58'00"E, under *Ficus* bark, 29 May 1992, M.S. Harvey, J.M. Waldock (MAGNT).

Paratypes. AUSTRALIA: *Northern Territory:* 8 males, 3 female, 1 tritonymph, same data as holotype (WAM T78992–T79003); 1 male, 1 female, same data as holotype (MAGNT); 1 male, same data as holotype (CAS); 1 male, same data as holotype (QM S90005).

Other material. AUSTRALIA: *Northern Territory*: 1 male, Batchelor [13°02'S, 131°01'E], 10 July 1914, G.F. Hill (NMV).

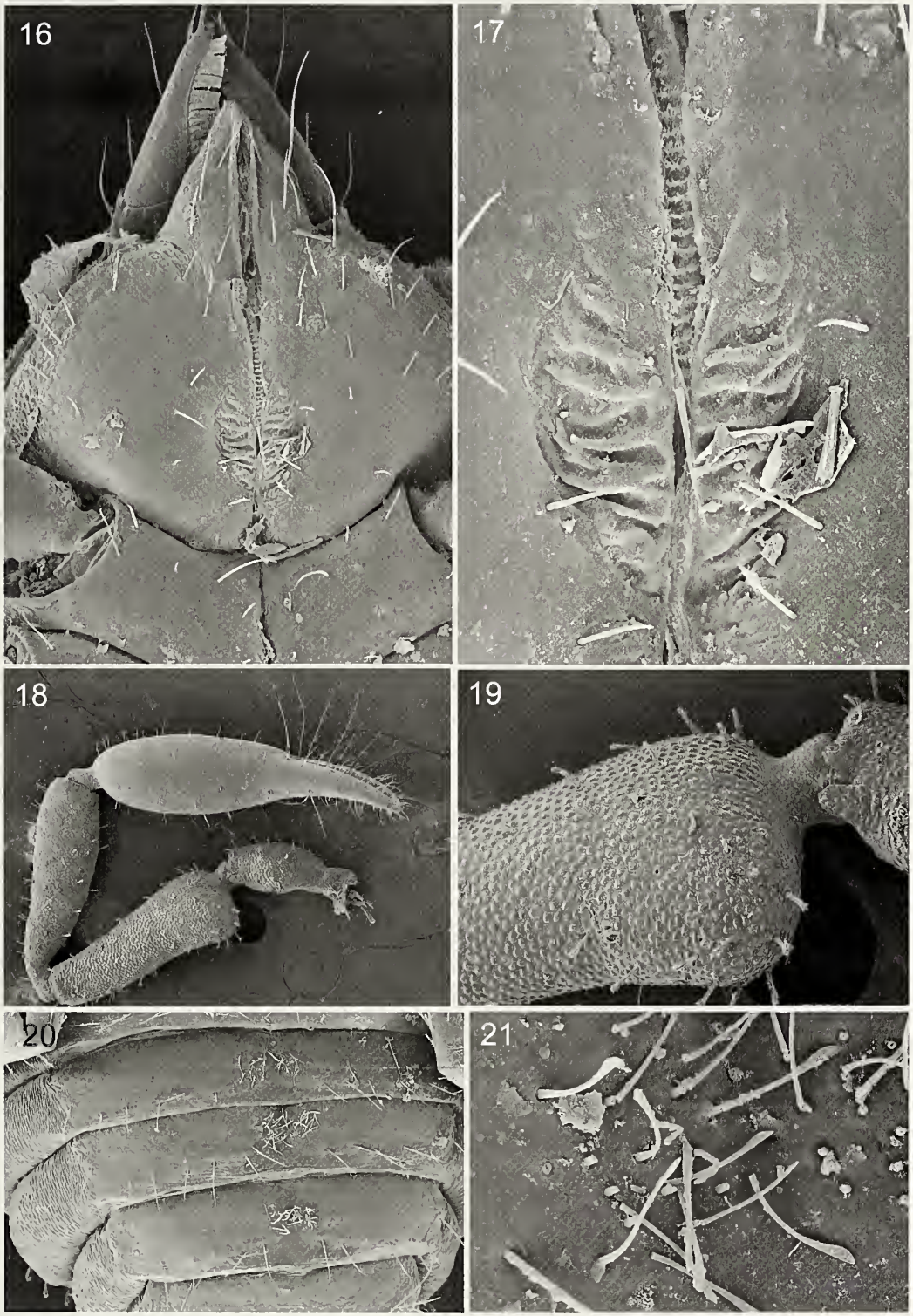
Figure 15.—*Rugowithius bulbosus* sp. nov., paratype male, dorsal.

Diagnosis.—Males of *Rugowithius bulbosus* are slightly smaller than *R. longissimus*, e.g. chela (with pedicel) 0.944–1.115 mm in length, the pedipalpal patella is less slender, 3.77–4.43 × longer than broad, and there are fewer glandular setae on male sternites IV–IX, i.e. 29: 46: 50: 38. Females appear to be indistinguishable from those of *R. longissimus*.

Description.—*Adults:* Colour (Fig. 15): with sclerotized portions generally dark red-brown; carapaceal metazone without paired pale spots.

Chelicera (Fig. 25): With 5 setae on hand, *bs* and *sbs* slightly dentate; movable finger with 1 subdistal seta; galea of male with 2 or 3 small terminal rami, of female with ca. 6 small terminal rami; rallum of 4 blades, the most distal blade with several serrations on leading edge, other blades smooth (Fig. 26); serrula exterior with 16 (♂), 17 (♀) blades; lamina exterior present.

Pedipalp (Figs. 23, 24): Trochanter, femur and patella granulate, chela completely smooth; dorsal setae clavate and denticulate; trochanter 1.76–1.94 (♂), 1.86–2.00 (♀), femur 2.64–2.83 (♂), 3.26–3.61 (♀), patella 3.77–4.43 (♂), 2.65–3.29 (♀), chela (with pedicel) 3.60–3.96 (♂), 2.97–3.05 (♀), chela (without pedicel) 3.36–3.71 (♂), 2.75–2.85 (♀), hand 1.95–2.25 (♂), 1.67–1.71 (♀) x longer than broad, movable finger 0.66–0.76 (♂), 0.61–0.74 (♀) x longer than hand. Femur of male with basal region greatly expanded (Fig. 24). Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Fig. 29): *eb* and *esb* situated basally; trichobothria *ib*, *ist*, *isb* and *it* grouped in basal half of finger; *b* and *sb* situated near one another; *st* slightly closer to *t* than to *sb*. Venom apparatus present in both chelal fingers, venom ducts long, terminating in nodus ramosus slightly basal to *et* in fixed finger and distal to *t* in movable finger. External margin of fixed finger with 2 sense-spots situated slightly anterior to *esb*; external margin of movable finger with three sense-spots, two slightly anterior to *sb*, and

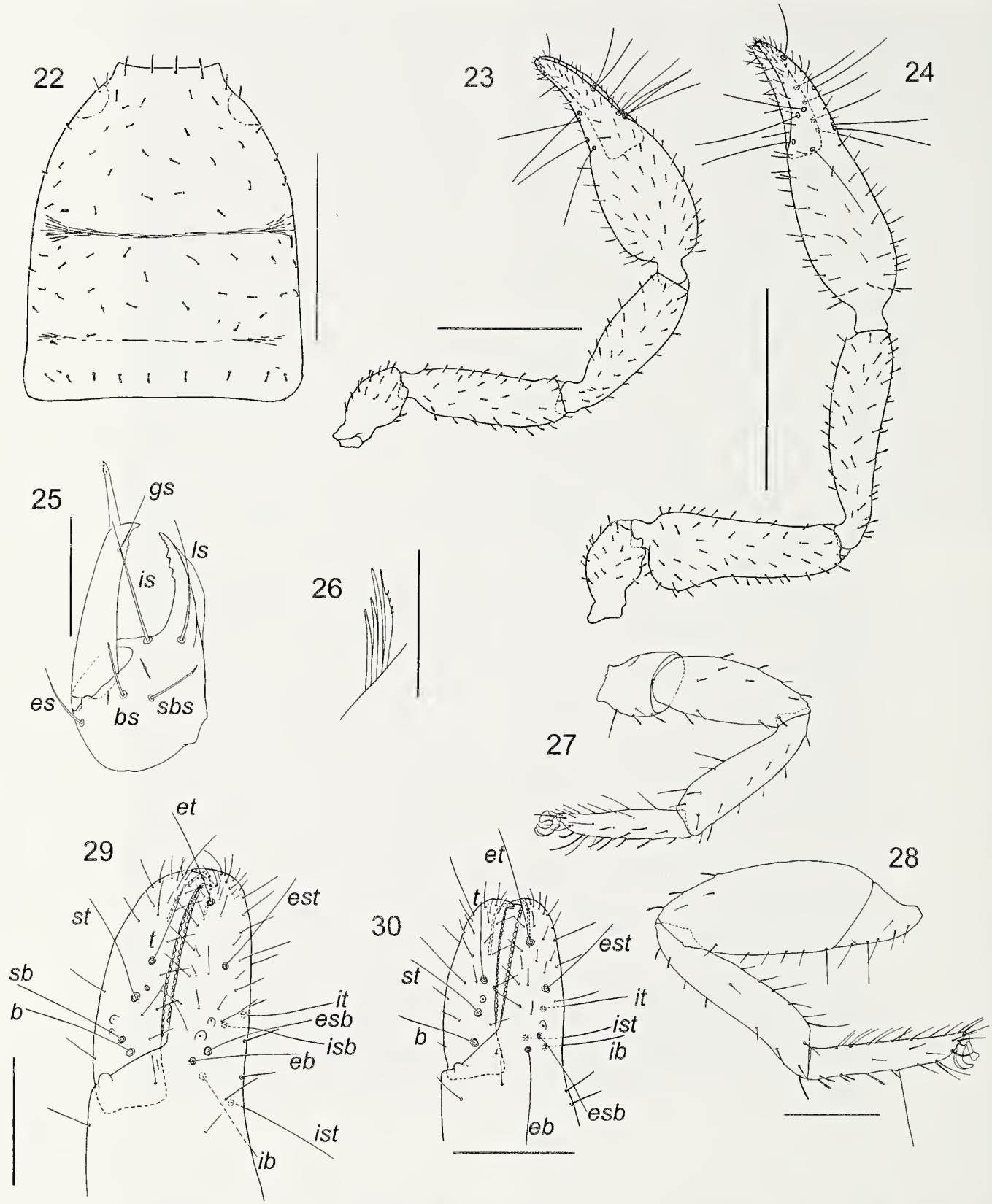


Figures 16–21.—*Rugowithius bulbosus* sp. nov., paratype male, scanning electron micrographs: 16. Maxillae; 17. Detail of central area showing rugose region; 18. Left pedipalp, dorsal; 19. Detail of base of pedipalpal femur; 20. Posterior sternites, ventral; 21. Detail of glandular setae.

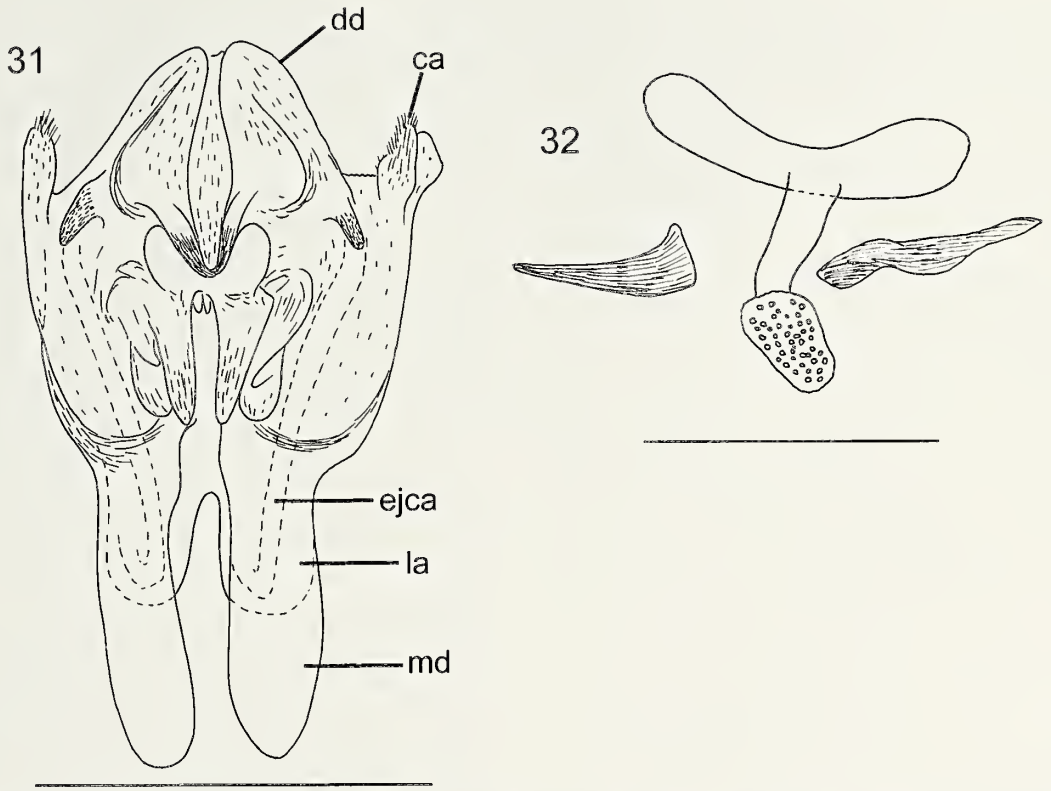
the other slightly anterior to *st*. Chelal teeth rounded; fixed finger with 30 (♂), 26 (♀) teeth; movable finger with 29 (♂), 28 (♀) teeth; accessory teeth absent.

Carapace (Fig. 22): 1.21–1.30 (♂), 1.27–1.28 (♀) x longer than broad; lateral margins slightly convex, not posteriorly widened; with 2 non-corneate eyes; with *ca.* 79 (♂), 75 (♀) setae, including 6 near anterior margin and 9 (♂), 11 (♀) near posterior margin; with 2 furrows, with distinct anterior furrow and indistinct posterior furrow; posterior furrow slightly closer to posterior carapaceal margin than to median furrow.

Coxal region: Maxilla with 2 apical setae and 1 very small internal, sub-oral seta (Fig. 16); externo-median region of male maxilla with patch of rugose cuticle (Fig. 17), females without patch; chaetotaxy of coxae I–IV: ♂, 11: 9: 7: 17, ♀, 11: 7: 6: 15.



Figures 22–30.—*Rugowithius bulbosus* sp. nov., holotype male unless stated otherwise: 22. Carapace, dorsal; 23. Right pedipalp, dorsal, paratype female (WAM T79000); 24. Right pedipalp, dorsal; 25. Left chelicera, paratype female (WAM T79000); 26. Rallum; 27. Left leg I; 28. Left leg IV; 29. Left chela, lateral; 30. Left chela, lateral, paratype tritonymph (WAM T79003). Scale lines = 0.5 mm (Figures 23, 24), 0.2 mm (Figures 22, 27, 28, 30), 0.1 mm (Figures 29, 25, 26).



Figures 31–32.—*Rugowithius bulbosus* sp. nov.: 31. Genitalia, dorsal, holotype male; 32. Genitalia, ventral, paratype female (WAM T79000). Scale lines = 0.2 mm (Figure 31), 0.02 mm (Figure 32).

Legs (Figs. 27, 28): Junction between femora and patellae I and II only slightly oblique; femur + patella of leg IV 2.78 (♂), 3.04 (♀) x longer than broad; tarsal tactile seta of leg IV situated sub-medially (Fig. 28), 0.58 (♂), 0.63 (♀) of tarsus length; subterminal tarsal setae arcuate and acute; arolium slightly shorter than claws.

Abdomen: Tergites and sternites with faint medial suture. Tergal chaetotaxy: ♂, 11: 11: 10: 12: 16: 15: 17: 15: 17: 13: 12 (including 2 tactile setae): 2; ♀, 9: 13: 11: 14: 17: 18: 14: 17: 14: 14: 11 (including 2 tactile setae): 2; mostly uniseriate but some tergites with a few setae placed anteriorly; all setae foliate. Sternal chaetotaxy: ♂, 7: (1) 9 (1): (1) 10 (1): 17: 20 + ca. 29 gls: 17 + ca. 46 gls: 15 + ca. 50 gls: 13 + ca. 38 gls: 12 (including 2 tactile setae): 12 (including 4 tactile setae): 2; ♀, 15: (1) 9 (1): (2) 12 (2): 14: 18: 17: 16 + 1/1 gls: 16 + 1/1 gls: 12 (including 2 tactile setae): 12 (including 4 tactile setae): 2; sternites VI–IX of male with patches of glandular setae (Fig. 20); sternites VIII–IX of female with 2 glandular setae; setae uniseriate and acuminate, except for smaller setae on sternite XI which are denticulate; glandular setae of male, long and distally spatulate (Fig. 21); male without paired invaginations on anterior margins of sternites.

Genitalia: Male with elongated and posteriorly rounded lateral apodemes (Fig. 31); female with T-shaped spermathecae (Fig. 32), receptacula not coiled and with large central cribriform plate and a pair of large triangular apodemes.

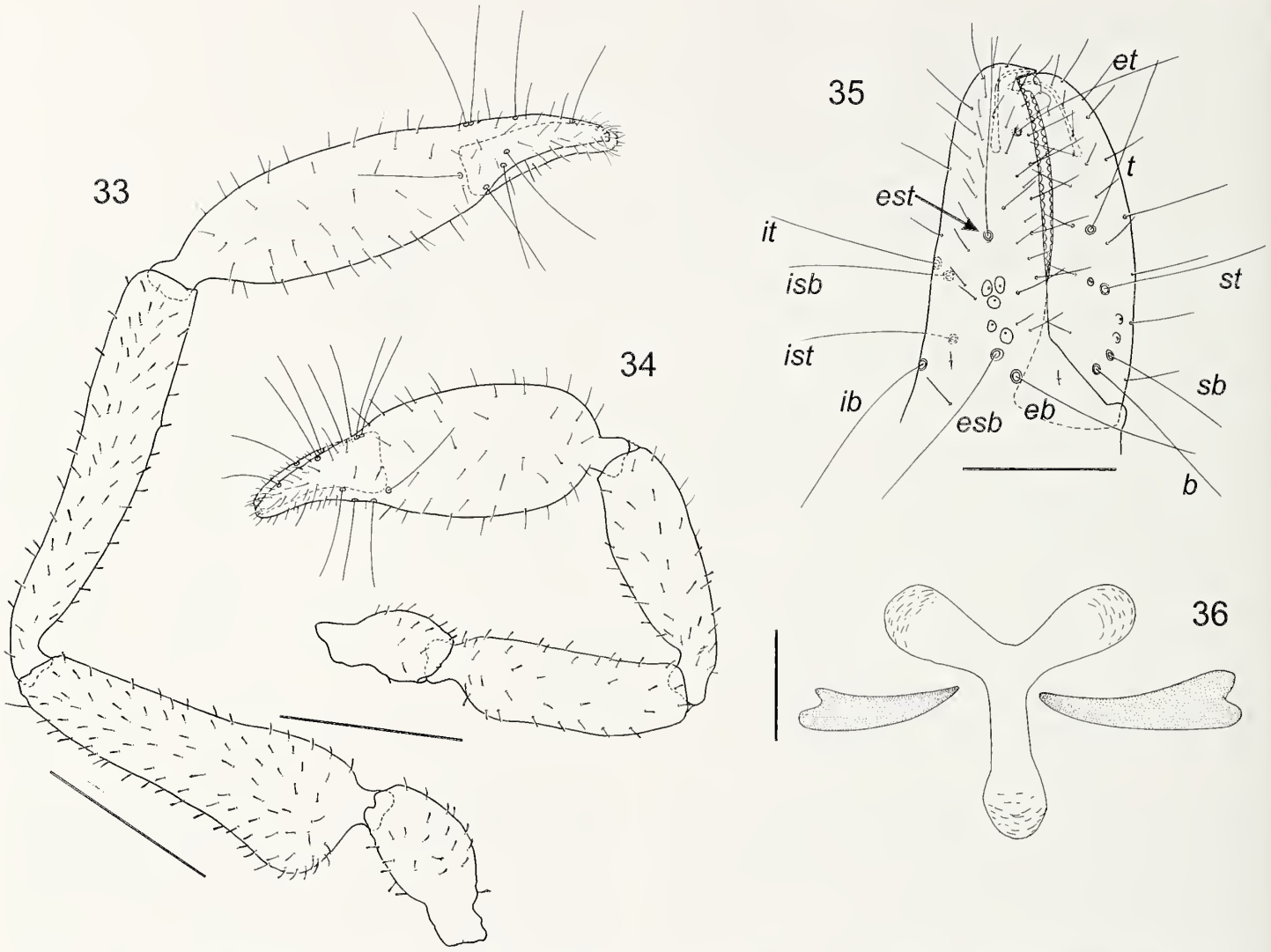
Dimensions (mm): Males: holotype followed by other males (where applicable): body length 2.00 (1.95–2.08). Pedipalps: trochanter 0.365/0.188 (0.304–0.371/0.173–0.191), femur 0.763/0.281 (0.627–0.797/0.225–0.282), patella 0.824/0.193 (0.678–0.864/0.174–0.195), chela (with pedicel) 1.104/0.290 (0.944–1.115/0.262–0.288), chela (without pedicel) 1.024 (0.880–1.024), hand length 0.592 (0.512–0.624), movable finger length 0.448 (0.369–0.410). Chelicera 0.216/0.120, movable finger length 0.163. Carapace 0.739/0.569 (0.646–0.659/0.499–0.536) (width at medial area); eye diameter 0.045. Leg I: femur 0.181/0.128, patella 0.327/0.129, tibia 0.344/0.094, tarsus 0.252/0.061. Leg IV: femur + patella 0.550/0.198, tibia 0.447/0.102, tarsus 0.339/0.065, TS 0.195.

Females: Paratype (WAM T79000) followed by other females (where applicable): body length 2.61 (1.60–2.91). Pedipalps: trochanter 0.326/0.175 (0.310–0.376/0.165–0.195), femur 0.621/0.172 (0.584–0.700/0.179–0.211), patella 0.627/0.192 (0.538–0.756/0.198–0.230), chela (with pedicel) 0.928/0.304 (0.930–1.109/0.311–0.364), chela (without pedicel) 0.866 (0.860–1.038), hand length 0.513 (0.518–0.621), movable finger length 0.378 (0.322–0.410). Chelicera 0.218/0.119, movable finger length 0.166. Carapace 0.691/0.540 (0.662–0.774/0.522–0.530) (width at medial area); eye diameter 0.080. Leg I: femur 0.138/0.115, patella 0.279/0.110, tibia 0.269/0.072, tarsus 0.280/0.052. Leg IV: femur + patella 0.526/0.173, tibia 0.428/0.090, tarsus 0.335/0.064, TS 0.211.

Tritonymph (WAM T79003): Colour: paler than adults.

Chelicera: With 5 setae on hand and a single seta (*gs*) on movable finger; rallum with 4 blades, the anterior blade with 4 spinules on anterior face, other blades smooth.

Pedipalp: Trochanter 2.05, femur 3.07, patella 2.88, chela (with pedicel) 3.01, chela (without pedicel) 2.84, hand 1.59 x longer than broad. Fixed chelal finger with 7 trichobothria, movable chelal finger with 3 trichobothria (Fig. 30): *isb* and *sb* absent.



Figures 33–36.—*Rugowithius longissimus* sp. nov., holotype male unless stated otherwise: 33. Left pedipalp, dorsal; 34. Right pedipalp, dorsal, paratype female; 35. Left chela, lateral; 36. Spermathecae, ventral, paratype female. Scale lines = 0.5 mm (Figures 33, 34), 0.2 mm (Figure 35), 0.02 mm (Figure 36).

Carapace: 1.22 x longer than broad; with 2 non-corneate eyes; with ca. 45 setae, including 6 near anterior margin and 8 near posterior margin; with 1 furrow, the posterior furrow apparently absent.

Legs: TS = 0.52.

Abdomen: Tergal chaetotaxy: 6: 6: 8: 10: 10: 10: 10: 10: 10: 9: 10 (including 4 tactile setae): 2. Sternal chaetotaxy: 4: (1) 4 (1): (2) 4 (2): 10: 9: 10 + 1/1 gls: 11 + 1/1gls: 9: 9 (including 2 tactile setae): 8 (including 4 tactile setae): 2; sternites VII–VIII each with 2 glandular setae.

Dimensions (mm): Body length 1.71. Pedipalps: trochanter 0.262/0.128, femur 0.454/0.148, patella 0.444/0.154, chela (with pedicel) 0.674/0.224, chela (without pedicel) 0.636, hand length 0.357, movable finger length 0.275. Carapace 0.499/0.410.

Remarks.—*Rugowithius bulbosus* is known only from two localities in the Northern Territory. The type specimens were taken from a small patch of rainforest on the edge of the East Alligator River where they were found under small pieces of tight-fitting bark of a fig tree (*Ficus* sp). Searches for this species in other rainforest patches in the Northern Territory has failed to uncover any further specimens of *R. bulbosus*, suggesting that this species may represent a short-range endemic species (Harvey 2002).

Etymology.—The specific epithet refers to the swollen basal region of the pedipalpal femur (*bulbosus*, Latin, swollen).

Rugowithius longissimus sp. nov.
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:C50F379B-EE51-4673-9EF8-CBE43F8E2037
Figs. 33–36

Material examined.—*Holotype.* AUSTRALIA: *Queensland:* male, 20 km N. of Cape Tribulation, 15°54'S, 145°29'E, 200 m, logs, 2 December 1990, Monteith, Sheridan and Thompson (QM S27199).

Paratypes. AUSTRALIA: *Queensland:* 1 male, same data as holotype (QM S90006); 1 female, Home Rule, Wallaby Creek, 15°45'S, 145°18'E, beating, 13 November 1974, V.E. Davies, K. McDonald (QM S27201).

Diagnosis.—Males of *Rugowithius longissimus* are slightly larger than those of *R. bulbosus*, e.g., chela (with pedicel) 1.189–1.344 mm in length (Fig. 37), the pedipalpal patella is more slender, 4.92–5.60 x longer than broad, and there are more glandular setae on male sternites IV–IX, i.e. 52: 61: 68: 58. Females appear to be indistinguishable from those of *R. bulbosus*.

Description.—*Adults:* Colour: dark red-brown; carapaceal uniformly coloured.

Chelicera: With 5 setae on hand, *bs* and *sbs* slightly dentate; movable finger with 1 subdistal seta; galea of male with 2 or 3 small terminal rami, that of female with 6 small terminal rami; rallum of 4 blades, the most distal blade with several serrations on leading edge, other blades smooth; serrula exterior with 17 (♂), 19 (♀) blades; lamina exterior present.

Pedipalp (Figs. 33, 34): Trochanter, femur and patella granulate, chela smooth; dorsal setae clavate and denticulate; trochanter 1.94–2.08 (♂), 1.97 (♀), femur 2.77–3.00 (♂), 3.44 (♀), patella 4.92–5.60 (♂), 3.18 (♀), chela (with pedicel) 3.77–4.20 (♂), 2.83 (♀), chela (without pedicel) 3.50–3.89 (♂), 2.64 (♀), hand 2.25–2.61 (♂), 1.72 (♀) x longer than broad, movable finger 0.53 (♂), 0.54 (♀) x longer than hand. Femur of male with basal region greatly expanded (Fig. 33). Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Fig. 35): *eb* and *esb* situated basally; trichobothria *ib*, *ist*, *isb* and *it* grouped in basal half of finger; *b* and *sb* situated near one another; *st* midway between *t* and *sb*. Venom apparatus present in both chelal fingers, venom ducts long, terminating in nodus ramosus slightly basal to *et* in fixed finger and distal to *t* in movable finger. External margin of fixed finger with 5 (♂), 4 (♀) sense-spots situated between *esb* and *est*; external margin of movable finger with 2 sense-spots situated between *sb* and *st*, and 1 situated adjacent to *st*. Chelal teeth rounded; fixed finger with 27 (♂), 22 (♀) teeth; movable finger with 26 (♂), 25 (♀) teeth; accessory teeth absent.

Carapace: 1.19–1.29 (♂), 1.25 (♀) x longer than broad; lateral margins slightly convex, not posteriorly widened; with 2 non-corneate eyes; with *ca.* 75 (♂), 63 (♀) setae, including 4 near anterior margin and 9 near posterior margin; with 1 furrow situated medially, posterior furrow absent.

Coxal region: pedipalpal coxa with 2 apical setae and 1 very small internal, sub-oral seta, externo-median region of male maxilla with rugose area; chaetotaxy of coxae I–IV: ♂, 10: 7: 8: 21; ♀, 11: 7: 7: 17.

Legs: Junction between femora and patellae I and II only slightly oblique; femur + patella of leg IV 2.93 (♂), 2.80 (♀) x longer than broad; tarsal tactile seta of leg IV situated submedially, 0.63 (♂), 0.61 (♀) of tarsus length; subterminal tarsal setae arcuate and acute; arolium slightly shorter than claws.

Abdomen: Tergites and sternites with faint medial suture. Tergal chaetotaxy: ♂, 11: 12: 10: 14: 17: 18: 17: 18: 14: 14: 10 (including 2 tactile setae): 2; ♀, 12: 11: 11: 16: 18: 17: 17: 17: 16: 14: 4 (arranged T2T): 2; mostly uniseriate but some tergites with a few setae placed anteriorly; all setae foliate. Sternal chaetotaxy: ♂, 9: (1) 10 (1): (2) 12 (2): 18: 28 + ca. 27/25 gls: 17 + ca. 32/29 gls: 14 + ca. 33/35 gls: 14 + ca. 29/29 gls: 15 (including 2 tactile setae): 16 (including 4 tactile setae): 2; ♀, 10: (1) 9 (1): (2) 15 (2): 18: 17: 17: 18: 17: 14 (including 2 tactile setae): 11 (including 4 tactile setae): 2; sternites VI–IX of male with patches of glandular setae, those on paratype male arranged ca. 27/23: ca. 31/28: ca. 27/33: ca. 29/29, respectively; sternites VII–VIII of female without glandular setae; setae uniseriate and acuminate; glandular setae long and distally spatulate; male without paired invaginations on anterior margins of sternites.

Genitalia: Male with elongated and posteriorly rounded lateral apodemes; female with T-shaped spermathecae (Fig. 36), receptacula not coiled, with a pair of large triangular apodemes.

Dimensions (mm): Males: holotype followed by paratype (where applicable): body length 2.85 (2.50). Pedipalps: trochanter 0.493/0.237 (0.422/0.218), femur 1.056/0.352 (0.883/0.319), patella 1.187/0.212 (1.024/0.208), chela (with pedicel) 1.344/0.320 (1.189/0.315), chela (without pedicel) 1.245 (1.102), hand length 0.834 (0.710), movable finger length 0.442 (0.378). Chelicera 0.256/0.138, movable finger length 0.186. Carapace 0.816/0.685 (0.754/0.584); eye diameter 0.083. Leg I: femur 0.179/0.166, patella 0.365/0.165, tibia 0.400/0.108, tarsus 0.316/0.069. Leg IV: femur + patella 0.672/0.229, tibia 0.522/0.128, tarsus 0.397/0.071, TS 0.250.

Female: Paratype: body length 2.24. Pedipalps: trochanter 0.359/0.182, femur 0.725/0.211, patella 0.726/0.228, chela (with pedicel) 1.024/0.362, chela (without pedicel) 0.954, hand length 0.623, movable finger length 0.339. Chelicera 0.219/0.122, movable finger length 0.181. Carapace 0.768/0.614; eye diameter 0.075. Leg I: femur 0.185/0.146, patella 0.334/0.154, tibia 0.310/0.096, tarsus 0.266/0.058. Leg IV: femur + patella 0.566/0.202, tibia 0.467/0.109, tarsus 0.358/0.069, TS 0.218.

Remarks.—*Rugowithius longissimus* is only known from two localities in north-eastern Queensland, each of which is dominated by rainforest habitats.

Etymology.—The specific epithet refers to the large size of this species in comparison with *R. bulbosus* (*longissimus*, Latin, longest).

Microwithius Redikorzev, 1938

Microwithius Redikorzev 1938:106.

Type species.—*Microwithius yurii* Redikorzev, 1938, by monotypy.

Diagnosis.—Males of *Microwithius* differ from all other genera of Withiidae by the presence of two discrete rounded patches of glandular setae on either side of the mid-line of sternites VII, VIII and IX (Harvey 1988, fig. 84).

Description.—Setae: most dorsal setae strongly clavate and denticulate; setae on sternites acicular.

Chelicera: With 5 setae on hand, *bs* and *sbs* denticulate, *es*, *ls* and *is* acuminate; movable finger with 1 subdistal seta (*gs*); rallum of 4 blades, the most distal blade with several serrations on leading edge, other blades smooth; lamina exterior present.

Pedipalp: Not sexually dimorphic; femur without hypertrophied base. Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria; trichobothria *ib*, *ist*, *isb* and *it* grouped in basal half of finger. Venom apparatus present in both chelal fingers, venom ducts long, terminating in nodus ramosus slightly basal to *et* in fixed finger and distal to *t* in movable finger. Chelal teeth all closely spaced; accessory teeth absent.

Carapace: With 2 non-corneate eyes; median furrow present, posterior furrow absent.

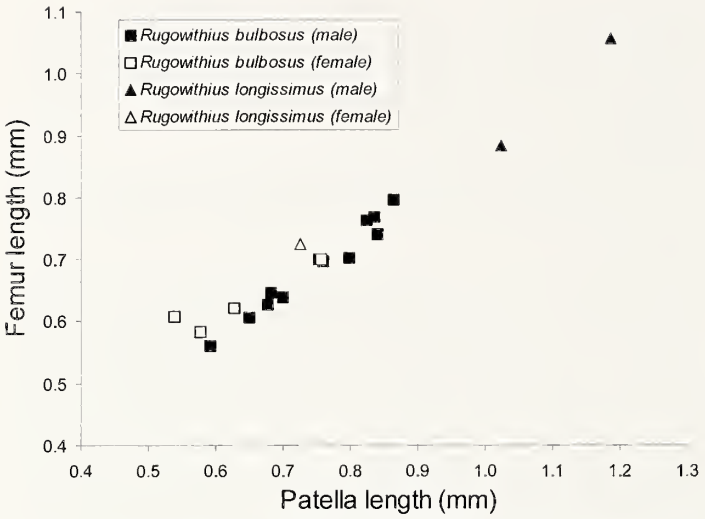


Figure 37.—Graph depicting the size of *Rugowithius bulbosus* sp. nov. and *R. longissimus* sp. nov.

Coxal region: Median maxillary lyrifissure present and submedially situated; sub-oral seta of maxilla not on 'hooked' mound; males without patch of ridged cuticle on internal margin of maxilla.

Legs: Junction between femora and patellae I and II only slightly oblique; tactile seta of posterior legs sub-medial; subterminal tarsal setae arcuate and acute; arolium slightly shorter than claws; claws slender and simple.

Abdomen: Tergites II–IX with medial suture, sternites V–X with faint medial suture. Male tergites without lateral keels. Males without paired sac-like invaginations on anterior margins of sternites; males with patches of glandular setae on sternites VII–IX, females with 2 glandular setae on sternites VII–IX; glandular setae of male short and conical. Spiracular helix present. Pleural membrane longitudinally striate and somewhat wrinkled.

Genitalia: Male genitalia with lateral apodemes long and triangular; female genitalia with 1 pair of coiled spermathecae.

Remarks.—The genus *Microwithius* was proposed by Redikorzev (1938) for the southeast Asian species *M. yurii* Redikorzev. Beier (1955b) added a second species, *M. tweediei*, from Malaysia and reduced *Microwithius* to a subgenus of *Metawithius*, noting that *M. tweediei* possessed intermediate character states similar to those of species of *Metawithius*. Sivaraman (1980) added two new species from India, *M. chamundiensis* Sivaraman, 1980 and *M. bulli* Sivaraman, 1980. As discussed above, males of the species here assigned to *Metawithius* possess a rugose patch on the internal surface of the maxilla, and the sub-oral seta is borne on a small hooked process on the internal maxillary margin (Fig. 5). These modifications are lacking in *Microwithius yurii* (Fig. 38), as are the features that are peculiar to members of the genus *Rugowithius*. Accordingly, *Microwithius* is here returned to full generic level as first proposed by Redikorzev (1938). The relationships of *Microwithius* to other withiid genera are uncertain and a thorough review of the Old World genera of Withiidae is necessary before any potential sister-group can be recognised.

Apart from the type species *M. yurii* from southeast Asia and Indonesia (see redescription by Harvey 1988), three Indian species are here included in the genus *Microwithius*: *M. indicus* (Murthy & Ananthakrishnan, 1977), **comb. nov.** from Tamil Nadu State, and *M. chamundiensis* (Sivaraman, 1980), **comb. nov.** and *M. bulli* (Sivaraman, 1980), **comb. nov.** both from Karnataka State. These generic transfers are justified on the grounds that males have two discrete rounded patches of glandular setae on either side of the mid-line of sternites VII, VIII and IX (Murthy & Ananthakrishnan 1977; Sivaraman 1980), a pattern that conforms to that found in *M. yurii* (Harvey 1988), but differs from those found in *Metawithius* where the glandular setae are laterally dispersed and tending to merge medially (Fig. 10). These Indian species require further study to ascertain their status as the original descriptions and illustrations are inadequate to fully separate them from each other or from *M. yurii*. The only other species previously included in *Metawithius (Microwithius)*, *M. tweediei*, does not belong in the genus *Microwithius*, and is treated below in the genus *Withius*.

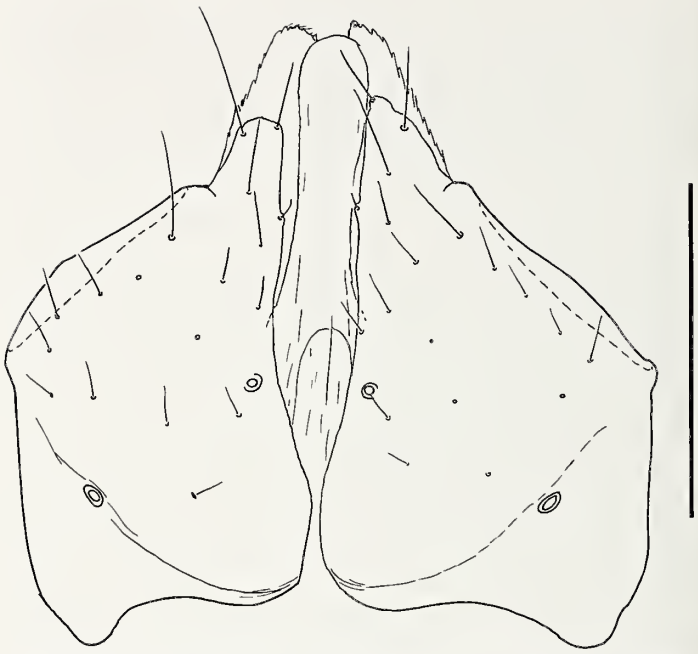


Figure 38.—*Microwithius yurii* Redikorzev, male (NMV), maxilla, ventral. Scale line = 0.2 mm.

Microwithius yurii Redikorzev, 1938
Fig. 38

Microwithius yurii Redikorzev 1938:106–108, figs. 35–38.

Material examined.—INDONESIA: *Jawa Barat*: 1 male, Krakatau Islands, Sertung, east ridge, 6°05'S, 105°23'E, 11 September 1984, beating in rainforest, 1984 Zoological Expedition Krakataus (NMV); 1 female, Krakatau Islands, Panjang, 6°05'S, 105°28'E, 25 September 1986, 1986 Zoological Expedition Krakataus (WAM T62538).

Description.—See Harvey (1988).

Remarks.—*Microwithius yurii* has been recorded from Cambodia, Indonesia and Vietnam (Redikorzev 1938; Harvey 1988). One of the four syntype male specimens of *M. yurii* from Vietnam was examined by (Harvey 1988).

Genus *Withius* Kew, 1911

Chelifer (Withius) Kew 1911:49.
Afrowithius Chamberlin 1931b:293. **Syn. nov.**
Allowithius Beier 1932b:53 (synonymized by Beier 1979: 107).
Xenowithius Beier 1953:75–76 (synonymized by Mahnert 1988: 65).

Type species.—*Withius: Chelifer subruber* Simon, 1879 (junior synonym of *Chelifer piger* Simon, 1878) by original designation.

Afrowithius: *Chelifer paradoxus* Ellingsen, 1912, by original designation.

Allowithius: *Chelifer (Chelifer) simoni* Balzan, 1892, by original designation.

Xenowithius: *Xenowithius transvaalensis* Beier, 1953, by original designation.

Diagnosis.—The majority of *Withius* species most closely resemble the *Aisthetowithius*, *Cryptowithius*, *Girardwithius*, *Ectromachernes*, *Juxtachelifer*, *Nannowithius*, *Stenowithius*, *Nesowithius*, *Parallowithius*, *Plesiowithius*, *Pogonowithius*, *Scotowithius*, *Sphallowithius*, *Stenowithius* and *Terunitowithius* as they all lack the long triangular lateral apodemes of the male genitalia. They differ from *Juxtachelifer* and *Terunitowithius* by the presence of glandular setae on the abdominal sternites (absent in *Juxtachelifer* and *Terunitowithius*); from *Nannowithius* by the presence of a tactile seta on tarsi III and IV (absent in *Nannowithius*); from *Girardwithius* by the straight chelal tooth rows (curved in *Girardwithius*); from *Ectromachernes* by the lack of a prolateral tubercle on the pedipalpal femur of males (present in *Cyrtowithius* and most *Ectromachernes*); from *Nesowithius* by trichobothrium *est* being equidistant between *esb* and *et* (closer to *esb* in *Nesowithius*); from *Stenowithius* by trichobothrium *it* being distal of *ist* and *est* (on same level as *ist* and *est* in *Stenowithius*); from *Aisthetowithius* by the relatively straight carapaceal furrows (sinuate in *Aisthetowithius*); from *Sphallowithius* by the pedipalps not being sexually dimorphic (male pedipalps much larger than female in *Sphallowithius*); from *Cryptowithius* and *Parallowithius* by trichobothrium *st* closer to *t* than *sb*, or midway between *t* and *sb* (*st* closer to *sb* than *t* in *Parallowithius*); and from *Pogonowithius* by the distinct submedian furrow (barely visible in *Pogonowithius*).

Description.—Setae: most dorsal setae strongly clavate and denticulate; setae on sternites acicular.

Chelicera: With 5 setae on hand; movable finger with 1 subdistal seta (*gs*); rallum of 4 blades; lamina exterior present.

Pedipalp: Not sexually dimorphie; femur without hypertrophied base. Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria; trichobothria *ib*, *ist*, *isb* and *it* grouped in basal half of finger, or *isb* and *it* situated medially. Venom apparatus present in both chelal fingers, venom ducts long, terminating in nodus ramosus slightly basal to *et* in fixed finger and distal to *t* in movable finger. Chelal teeth all closely spaced; accessory teeth absent.

Carapace: With 2 corneate eyes; median and furrows present.

Coxal region: Median maxillary lyrifissure present and submedially situated; sub-oral seta of maxilla not on 'hooked' mound; males without pateh of ridged cuticle on internal margin of maxilla.

Legs: Junction between femora and patellae I and II only slightly oblique; tactile seta of posterior legs sub-medial; subterminal tarsal setae arcuate and acute; arolium slightly shorter than claws; claws slender and simple.

Abdomen: Male tergites without lateral keels; males without paired sac-like invaginations on anterior margins of sternites; males with patches of glandular setae on sternites V–IX, and sometimes on IV and X; females with 2 glandular setae on sternites VII–IX; glandular setae of male short and conical. Spiracular helix present. Pleural membrane longitudinally striate and somewhat wrinkled.

Genitalia: Male genitalia with shortened lateral apodemes, or with lateral apodemes long and triangular (but these species most likely misplaced in *Withius*); female genitalia with 1 pair of spermathecae.

Remarks.—As discussed elsewhere in this paper, the genus *Withius* is difficult to define and currently includes species that are most likely misplaced such as *W. hispanus*, *W. fanuus*, *W. neglectus* and *W. japonicus* which have totally different male genitalia to other species of the genus. Despite this uncertainty, the following two species are transferred to *Withius*.

Withius paradoxus (Ellingsen, 1912), comb. nov.

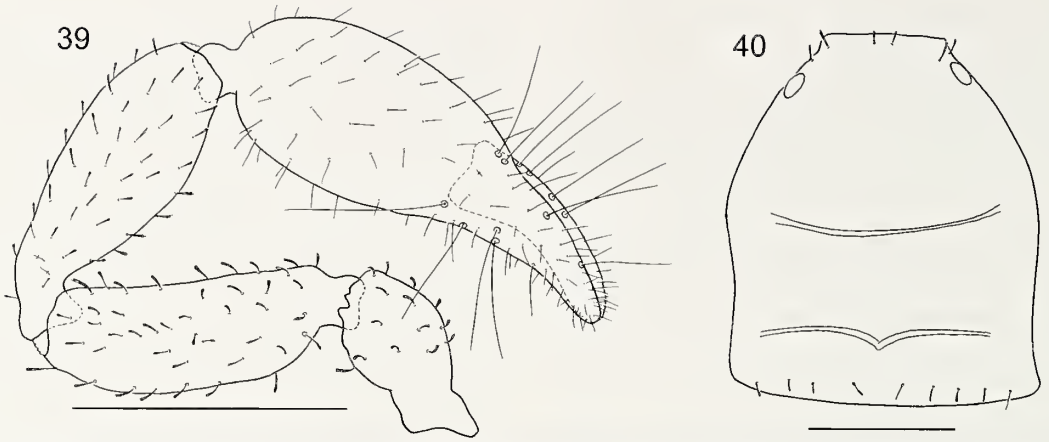
Chelifer paradoxus Ellingsen 1912:98–99.
Stenowithius crassipes Lawrence 1937:270–272, fig 30a–c. **Syn. nov.**

Material examined.—SOUTH AFRICA: *Eastern Cape*: 2 males, 2 females, 2 tritonymphs, Glenconnor [33°24'S, 25°09'E], iii.1964, R.F. Lawrence (NMP 7904); 1 male, 1 female, Grahamstown [33°19'S, 26°32'E] (CAS JC–237.01001–2).

Description.—See Mahnert (1988).

Remarks.—Ellingsen (1912) described *C. paradoxus* from three specimens collected in South Africa: the holotype (cited as the "type") from Ntaba Kandoda, near King Williams Town (32°52'S, 27°23'E), a male from Blythswood (32°13'S, 27°59'E) and a female from Kei Bridge (32°30'S, 27°59'E), all localities are nowadays situated in Eastern Cape Province. The specimens were collected by R. Godfrey and most likely returned to him (Ellingsen 1912, p. 90), although they could not be located in the Albany Museum, Grahamstown where Godfrey's collection was apparently lodged (J. Midgley, in litt., 11 March 2014) or in the South African Museum, Cape Town (M. Cochrane, in litt., 28 August 2009). The collections of the Albany Museum were extensively damaged in a fire in 1941 and it is possible that they were lost during this incident.

Two slide-mounted specimens labeled *Afrowithius paradoxus* by J.C. Chamberlin are lodged in CAS and were examined as part of this study. Although these specimens were not explicitly listed by Chamberlin (1931b) and are not type specimens, they were evidently used by Chamberlin when formulating his diagnosis of *Afrowithius*. These specimens conform quite closely to Ellingsen's description especially in the thickened male tibia IV which Ellingsen (1912) noted was "very broad (high), being very convex on the inner side". This feature is also characteristic of *Withius crassipes* (Lawrence 1937) (originally described as *Stenowithius crassipes*) which has an enlarged male tibia IV (Lawrence 1937; Beier 1958; Mahnert 1988). There are no appreciable differences between these specimens of *C. paradoxus* and *S. crassipes* and, therefore, *S. crassipes* is here



Figures 39–40.—*Withius tweediei* (Beier), lectotype male: 39. Left pedipalp, dorsal; 40. Carapace, dorsal. Scale lines = 0.5 mm (Figure 39), 0.25 mm (Figure 40).

designated as a junior subjective synonym of *C. paradoxus*. *Stenowithius crassipes* was originally described from Nkandhla Forest, in KwaZulu-Natal of South Africa, and has been subsequently recorded from other locations in South Africa (Beier 1958, 1964, 1966a) and central Kenya (Mahnert 1988).

Chamberlin (1931b) transferred *C. paradoxus* to the new monotypic genus *Afrowithius* which he distinguished from all other withiid genera by the presence of five blades in the chelicerae rallum. Whilst the male of *C. paradoxus* examined by Chamberlin (1931b) has one chelicera with five rallar blades, the other chelicera, and both chelicerae of the female, possesses the four blades typical of all Withiidae. Therefore, the main diagnostic feature distinguishing *Afrowithius* from other withiid genera is removed, and *Afrowithius* is considered to be a junior synonym of *Withius*. The male and female genitalia of Chamberlin's specimens and other specimens of this species are of the type that characterize species of *Withius* (Mahnert 1988).

Withius tweediei (Beier, 1955), comb. nov.
Figs. 39, 40

Metawithius (Microwithius) tweediei Beier 1955b:43–45, fig. 5.

Material examined.—*Lectotype.* MALAYSIA: *Pahang*: male, near Telom Valley, Gunung Siku, Cameron Highlands [4°36'N, 101°24'E], ca. 4500 feet elevation, March 1935, M. W.F. Tweedie (NHMW).

Paralectotypes. MALAYSIA: *Pahang*: 1 female, collected with lectotype (NHMW); 1 male, Kampung Kuala Terla, Telom Valley, Cameron Highlands [4°32'N, 101°25'E], ca. 4500 feet elevation, March 1935, M.W.F. Tweedie (NHMW).

Diagnosis.—*Withius tweediei* is most similar to those species of *Withius* in which trichobothria *isb* and *it* are clustered in the basal half of the fixed chelal finger. It lacks the male genitalic conformation of *W. fauuus*, *W. hispanus*, *W. japonicus* and *W. neglectus*, and has a different shaped chela than *W. despaxi* and *W. transvaalensis*.

Description.—*Adults:* Colour: with sclerotized portions generally dark red-brown; carapaceal metazone without paired pale spots.

Chelicera: With 5 setae on hand, *bs* and *sbs* slightly dentate; movable finger with 1 subdistal seta; galea of male with 3 small terminal rami, of female unknown (broken from only known specimen); rallum of 4 blades; serrula exterior with 16 (♂), 18 (♀) blades; lamina exterior present.

Pedipalp (Fig. 39): Trochanter, femur and patella granulate, chela smooth; dorsal setae clavate and denticulate; trochanter 1.72–2.06 (♂), 1.99 (♀), femur 2.93–2.95 (♂), 3.01 (♀), patella 2.88–3.03 (♂), 2.60 (♀), chela (with pedicel) 3.01–3.09 (♂), 2.86 (♀), chela (without pedicel) 2.82–2.88 (♂), 2.66 (♀), hand 1.68–1.73 (♂), 1.66 (♀) x longer than broad, movable finger 0.71–0.73 (♂), 0.59 (♀) x longer than hand. Femur of male with basal region not expanded. Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria: *eb* and *esb* situated basally; trichobothria *ib*, *ist*, *isb* and *it* grouped in basal half of finger; *b* and *sb* situated near one another; *st* slightly closer to *t* than to *sb*. Venom apparatus present in both chelal fingers, venom ducts long, terminating in nodus ramosus slightly basal to *et* in fixed finger and distal to *t* in movable finger.

Carapace (Fig. 40): 1.23–1.31 (♂), 1.17 (♀) x longer than broad; lateral margins strongly convex, not posteriorly widened; with 2 non-corneate, flat eye-spots; with numerous setae, including 5 (♂, ♀) near anterior margin and 9 (♂), 10 (♀) near posterior margin; with 2 furrows, with distinct anterior furrow and indistinct posterior furrow; posterior furrow slightly closer to posterior carapaceal margin than to median furrow.

Coxal region: Maxilla with 2 apical setae and 1 very small internal, sub-oral seta, externo-median region of male maxilla without rugose area; chaetotaxy of coxae I–IV: ♂, 9: 10: 8: 19, ♀, 9: 8: 9: 17.

Legs: Junction between femora and patellae I and II only slightly oblique; femur + patella of leg IV 2.51 (♂), 2.80 (♀) x longer than broad; tarsal tactile seta of leg IV situated submedially, 0.50 (♂), 0.57 (♀) of tarsus length; subterminal tarsal setae arcuate and acute; arolium slightly longer than claws.

Abdomen: Tergites and sternites with faint medial suture. Tergal chaetotaxy: ♂, 10: 10: 11: 11: 14: 13: 15: 14: 14: 15: 8 (including 2 tactile setae): 2; ♀, 12: 10: 11: 17: 17: 18: 16: 18: 17: 12: 8 (including 2 tactile setae): 2; mostly uniseriate but some tergites with a few setae placed anteriorly; all setae foliate. Sternal chaetotaxy: ♂, 8: (1) 8 (1): (2) 9 (2): 14 + ca. 20/20 gls: 11 + ca. 45/45 gls: 12 + ca. 40/40 gls: 10 + ca. 35/35 gls: 10 + 20/21 gls: 12 (including 2 tactile setae): 12 (including 4

tactile setae): 2; ♀, 8: (1) 8 (1): (2) 8 (2): 16 + 2/2 gls: 16 + 2/2 gls: 16 + 2/2 gls: 13 + 1/1 gls: 13 + 1/0/ gls: 12 (including 2 tactile setae): 14 (including 4 tactile setae): 2; sternites V–IX of male with patches of glandular setae; sternites V–IX of female with glandular setae; setae uniseriate and acuminate; glandular setae of male stout and conical; male without paired invaginations on anterior margins of sternites.

Genitalia: Male with lateral apodemes short, other details not visible in specimens; female spermathecae not observable in specimen.

Dimensions (mm): Males: Lectotype from Gunong Siku, followed by paralectotype male from Kampung Kuala Terla (where applicable): body length 2.10 (ca. 2.00). Pedipalps: trochanter 0.307/0.179 (0.408/0.198), femur 0.582/0.197 (0.626/0.214), patella 0.608/0.211 (0.685/0.226), chela (with pedicel) 0.884/0.294 (0.960/0.311), chela (without pedicel) 0.830 (0.896), hand length 0.493 (0.538), movable finger length 0.362 (0.384). Chelicera 0.217/0.103, movable finger length 0.173. Carapace 0.666/0.541 (0.752/0.576) (width at medial area); eye diameter 0.070. Leg IV: femur + patella 0.424/0.169, tarsus 0.300/0.064, TS 0.150.

Female: Paralectotype from Gunong Siku: body length 2.16. Pedipalps: trochanter 0.316/0.159, femur 0.512/0.170, patella 0.509/0.196, chela (with pedicel) 0.806/0.282, chela (without pedicel) 0.750, hand length 0.468, movable finger length 0.277. Chelicera 0.212/0.108, movable finger length 0.160. Carapace 0.608/0.518 (width at medial area); eye diameter 0.060. Leg IV: femur + patella 0.471/0.168, tarsus 0.314/0.032, TS 0.179.

Remarks.—The type series consists of three specimens, a pair of adults from Gunong Siku stated by Beier (1955b) to be "Types", and a paratype male from Kuala Terla. Beier frequently failed to segregate a single specimen from the type series as a holotype, and often referred to a vial with more than one specimen as the "types" and labelled the remaining specimens as "paratypes". As Beier clearly intended that the three specimens were not syntypes, I hereby designated the male from Gunong Siku as lectotype, and the other two specimens as paralectotypes. A search for further specimens in the vicinity of the two known localities in 2009, including sifting leaf litter and searching under the bark of trees and logs, failed to locate any further specimens.

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Cues guiding uloborid construction behavior support orb web monophyly

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Abstract. Behavior can provide useful traits for testing phylogenetic hypotheses, and some details of orb web construction behavior have been especially useful in characterizing higher-level groups in spiders. The cues used to guide construction behavior and behavioral responses to these cues hold similar promise, but have never been used in phylogenetic studies. Here we use several techniques to test the hypothesis that orb webs in the two major branches of orb-weaving araneomorph spiders (Araneoidea and Deinopoidea) are monophyletic, using both the cues that guide orb construction and the spiders' responses to these cues. If orb webs evolved only once, the expectation is that these traits should be similar in members of both evolutionary lines. This prediction was supported: species in the two groups use several of the same cues, and respond to them in similar ways. These cues include two identical reference stimuli for positioning sticky spiral lines; supplies of silk available in their glands that affect the positioning of sticky spiral loops; and at least one stimulus related to the size of the available space for the orb, which is used to trigger similar modifications of seven independent orb design traits. Neither group used tension-related cues to guide sticky spiral placement. These comparisons reinforce previous conclusions supporting orb web monophyly that were derived from morphological, molecular, and behavioral traits.

Keywords: Behavioral traits, phylogeny, orb web construction

The use of behavioral traits as taxonomic characters has a tangled history. Behavior is often highly variable and context-dependent, and it has been argued that its variability and putative diffieulties in determining homologies make it an unreliable indicator of relationships (Atz 1970; Ryan 1996). Several reviews indicate, however, that it is on average neither more nor less reliable than morphology (Roe & Simpson 1958; Wenzel 1992; deQuiroz & Wimberger 1993; Kuntner et al. 2008). The growing ability to collect video recordings and make them available in publications (e.g., Puniamoorthy et al. 2008) promises to promote more extensive use of behavior in systematic studies.

In spiders some behavioral traits are taxonomically informative, while others are less useful. On the one hand, some details of orb web construction constitute the least homoplasious group of traits yet found for deciphering the relationships among families and superfamilies of orb weavers (Kuntner et al. 2008; Lopardo et al. 2010). In contrast, the variation in non-orb webs in the family Theridiidae showed such a poor fit with a well-supported tree, which had been established previously on the basis of largely concordant morphological and molecular traits, that their analysis was described as "chaos from order" (Eberhard et al. 2008).

To our knowledge, previous taxonomic analyses of behavior have generally or exclusively utilized actions or behavior patterns and their results (e.g., web architecture). The present paper breaks new ground by concentrating not on actions *per se*, but rather on the stimuli that are used to direct and guide actions, and on the rules that determine the responses that animals make to these stimuli. This focus opens an additional, possibly independent dimension for exploration. It is feasible for a given behavioral activity to persist through evolutionary time but for the stimuli that are used to elicit or guide it to change. Thus, for instance, bembecine wasps all use their mandibles and forelegs to dig nesting holes in the ground; but the cues that elicit digging behavior presumably vary in groups that nest in different types of substrate (hard packed soil, sand, etc.) (Evans 1966). And, vice versa, the cues that elicit and guide an animal may remain unchanged even when the behavior itself changes. For instance, web-building spiders have eontinued to use the vibrations generated by their prey to guide their attack behavior, even while attack behavior has evolved from direet bites to wrapping with dry aciniform silk, and then to wrapping with viscid, aggregate gland silk (Barrantes & Eberhard 2007).

The possibility that behavioral actions and cues could evolve independently is particularly strong in orb weaving spiders. This is because the geometric regularity of an orb means that there are often several different types of potential cues, such as angles between lines, distances between lines, and vibrations or tensions that could be used to guide any particular decision during construction. For example, some species use multiple, largely redundant cues to guide decisions regarding sticky spiral placement (Eberhard & Hesselberg 2012). As a result, the cues and behavior involved in orb web construction offer a particularly attractive opportunity to use behavioral cues to examine an old, classic controversy coneerning the monophyletic or polyphyletic origin of orb webs. In this paper, we provide new data on the cues and responses in a species in one of the two major evolutionary lineage of orb weavers (Deinopoidea), and compare them with published data from the other, better-studied major orb-weaver lineage (the seven orb-weaving families of Araneoidea) to test the hypothesis that orb webs in these two lineages are monophyletic.

Taxonomic background.—There is a long history of controversy over whether orb webs evolved one or more times in the deinopoid and araneoid lineages. Strong similarities between the two groups in their basic orb designs, in the general stages of building behavior, and in the order of the stages were documented long ago, arguing for a single, monophyletic origin (Wiehle 1931). The major steps in the process of orb construction, and the order in which they are executed are uniform in all of the more than 100 species of orb weavers (both deinopoids and araneoids) that have now been observed building their webs: frame lines and radii are built

first, then more radii and hub lines; then more hub lines and the temporary spiral are added, working from the hub outward; and finally the sticky spiral is built from the edge of the web inward (summaries in Eberhard 1982, 1990; Kuntner et al. 2008). Observations of alternative construction stages and ordering of operations in other, non-orb weaving species (e.g., construction of the "rectangular orbs" of *Synotaxus* spp. Simon 1895) (Eberhard 1977, 1995) has shown that this consistency in orb weavers is not simply a result of construction constraints (Coddington 1986).

Nevertheless, dual origins for orb webs were suggested by the great taxonomic importance that was historically placed on the presence or absence of one compound morphological trait: a plate (the cribellum) that is formed from a modified pair of spinnerets, and the comb of bristles on the hind metatarsus (the calamistrum) that is used to comb the silk from this plate (Simon 1892). The likelihood that the orb design is highly adaptive (Witt 1965; Agnarsson et al. 2013), the high degree of flexibility in many aspects of orb design (Herberstein & Tso 2011), and the recent discovery of orb-like webs in the distantly related group *Fecenia* (Psechridae) (Bayer 2011; Agnarsson et al. 2013) all make convergence on orb designs seem less unlikely (for histories of these ideas, see Coddington (1986) and Shear (1986)).

Most recent phylogenetic analyses of morphological and behavioral traits (Griswold et al. 1998; Kuntner et al. 2008), as well as molecular traits (Garb et al. 2006; Blackledge et al. 2009; Dimitrov et al. 2012) have supported the single origin hypothesis for orb webs. The degree of support has been controversial, however (Dimitrov et al. 2012), and the question of how cribellate sticky lines evolved and replaced cribellate sticky lines without any known intermediate orb web forms that lacked sticky lines is still a puzzle (Opell & Schwend 2009).

Until last year, a general consensus that favored the single origin hypothesis for orb webs seemed to be emerging, based on morphological and behavioral (Griswold et al. 1998; Kuntner et al. 2008) as well as molecular traits (Garb et al. 2006; Blackledge et al. 2009; Dimitrov et al. 2012). In 2014, however, a pair of molecular analyses, which attempted to correct for several potential problems, including artificial inflation of support due to missing data, unequal rates of evolution in different lineages, compositional heterogeneity, and heterotachy (Fernandez et al. 2014, Bond et al. 2014), found support for linking the deinopoids more closely with a large group of about 40 non-orb weaving (and largely webless) families (the "RTA clade"), rather than with araneoids. If this grouping holds up under further tests, it would imply either multiple derivations of orb webs, or a single, even more ancient derivation and a subsequent loss of orbs in the ancestor of the RTA clade (the preferred hypothesis of Bond et al. 2014). In light of these uncertainties, further tests of the monophyly hypothesis based on additional traits are of interest.

Behavioral background.—During orb web construction spiders guide their behavior by sensing and responding to several different cues (Hingston 1920; Eberhard 1972, 1988a; Vollrath 1986, 1987, 1992; Eberhard & Hesselberg 2012). The cues that are used by araneoids to guide sticky spiral placement can be divided into two groups: "reference stimuli" that are perceived anew each time a spider arrives at the next radius (e.g., cues from the positions of the radius and the lines already attached to it); and "general settings" stimuli that are not associated with particular sites in the web (e.g., body size and weight of the spider, nutritional status, silk reserves, and the spider's general position in the web with respect to vertical, and to the hub vs. the edge). One reference stimulus that guides sticky spiral placement in araneoids was demonstrated nearly 100 years ago by the pioneer naturalist, R. W. G. Hingston. When he removed a segment of the inner loop of sticky spiral while the araneid spider *Neoscona nautica* (L. Koch 1875) was laying sticky spiral line (Fig. 1a: a "Hingston experiment" hereafter), Hingston found that the site of the inner loop of sticky spiral is used as a reference point (the "inner loop site" cue hereafter) to guide the placement of the following loop of sticky line: the next sticky spiral attachment was displaced outward on the radius to the site where he had experimentally broken the inner loop, while its placement was not altered on the preceding or the subsequent radius where the previous loop remained intact (Fig. 1a) (Hingston 1920).

Subsequent Hingston experiments with other species in the araneoid families Araneidae, Nephilidae and Tetragnathidae showed that they also use the inner loop site cue (Peters 1954; Eberhard & Hesselberg 2012). Additional, finer analyses of the results of Hingston experiments, in combination with experimental removal of segments of the temporary spiral and correlations in finished webs, showed that spiders also use a second reference cue, the distance from the outer loop of temporary spiral (the "temporary spiral distance" cue) to guide sticky spiral spacing in both an araneid and a tetragnathid (Eberhard 2011; Eberhard & Hesselberg 2012).

The experimental demonstration that the site of the inner loop of sticky spiral provides important reference cues during sticky spiral construction complements the behavioral observation concerning how many orb weavers move their legs during stieky spiral construction. Legs I and II are moved in ways that appear designed to locate the inner loop just before each sticky spiral attachment is made (the "inner loop localization behavior" of Eberhard 1982; Scharff & Coddington 1997; Kuntner et al. 2008). (It should be kept in mind that an orb weaver is effectively blind with respect to the lines in its web; tapping behavior with its legs is equivalent to a blind man tapping with his cane). Uloborid sticky spiral construction behavior includes similar inner loop localization behavior with its legs I (Eberhard 1972, 1982), suggesting that these spiders also use cues from the inner loop to guide sticky spiral placement; but Hingston experiments have never been performed with any uloborid.

The probable effects of one general settings cue—the amount of reserves of sticky silk in the spider's silk glands—were established by experimentally interrupting araneid and tetragnathid spiders after they had laid the non-sticky lines but before they laid the sticky lines in a new orb, removing the web, and then observing the design of the replacement webs that they built a few hours later (Eberhard 1988b). Webs built after this experimental treatment were larger in overall web size and had smaller distances between loops of sticky spiral than control webs that were built after removal of newly built complete orbs (thus allowing the spider to decrease its reserves of sticky silk).

Another recent experimental technique allowed comparative study of several additional responses in several araneoid

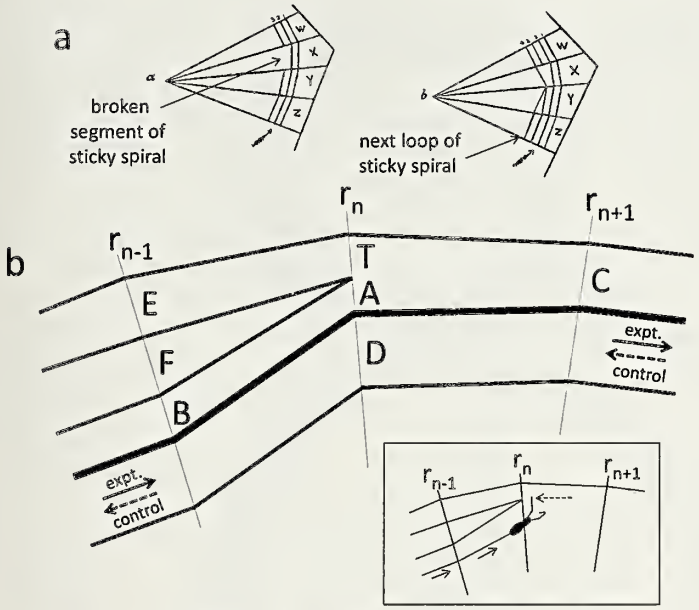


Figure 1.—a) Hingston's drawings illustrate that when he experimentally removed a segment of sticky spiral during sticky spiral construction (left), the araneid *Neoscona nautica* displaced the attachment of the next loop (loop 4 in b) outward on the radius (between X and Y) (right) (feathered arrow indicates the direction the spider moved) (from Hingston 1920). Judging by more recent observations, the outward deflection of the next loop was probably exaggerated in this drawing (see Eberhard & Hesselberg 2012). b) Schematic representation of distances associated with an encounter with a turn back that resulted in a spontaneous "Hingston experiment" in a *Z. geniculata* web. The thinnest lines are non-sticky radii, and thicker lines are sticky spiral lines; the thickest is the sticky spiral loop during whose construction a spontaneous "experiment" (or a "control") occurred. When the spider encountered the radius (r_n) on which a turn back had occurred while moving one direction ("expt." arrows), her ol failed to contact the inner loop of the turn back (dotted arrow in inset) during inner loop localization behavior, and an "experiment" occurred: the stimuli available to the spider were similar to those in a Hingston experiment in which the inner loop between r_n and r_{n+1} had been broken. In contrast, when the spider encountered a turn back while moving in the opposite direction ("control" arrows), leg ol did touch the inner line of the turn back; such encounters thus amounted to "controls". The monophyly hypothesis, that the uloborid uses the same cues in the same ways as araneoids, thus predicts that A would be smaller than B, C, and D in experimental encounters, and that it would be similar to B, C, and D in control encounters. Both predictions were fulfilled.

species. Spiders were induced to build orbs in small containers that severely restricted the spaces in which they could build, and this resulted in changes in several design features of the orbs they built in the araneids *Eustala illicita* (O. P.-Cambridge 1889) and *Cyclosa caroli* (Hentz 1850), the nephilid *Nephila clavipes* (Linnaeus 1767), and the tetragnathid *Leucauge argyra* (Walckenaer 1841) (Hesselberg 2010; Barrantes & Eberhard 2012). This technique has the disadvantage that the precise cue or cues that are used by the spider to sense the size of the space are not known; but it elicits up to seven apparently independent behavioral responses (Barrantes & Eberhard 2012). The expectation of the monophyly hypothesis is that the changes in uloborid orbs built in especially small containers will resemble the changes seen in the orbs of araneoids built in similarly restricted spaces.

Aims of this study.—The present study compares data from previous studies of araneoid and uloborid spiders, and new observations of a representative of the deinopoids, the uloborid *Zosis geniculata* (Olivier 1789). The monophyly hypothesis predicts that both the cues that spiders use and the responses that they give to these cues should be similar in deinopoids and araneoids. The degree of difference between uloborids and araneoids should not be substantially greater than that among the different families of araneoids. Extensive comparisons have not been possible before, because most of the previous experimental studies of the cues guiding orb construction behavior have involved only araneoids.

METHODS

General conditions.—We collected adult females of the synanthropic uloborid *Zosis geniculata* in buildings in San Rafael de Escazú (about 1000 m el.) and near Tárcoles, Costa Rica (about 20 m el.). We housed them individually in approximately cylindrical plastic containers of variable diameters (see below) whose upper, detachable rims (cut from similar containers) were lined with black paper that allowed spiders to walk easily and attach their lines. The open end at the top of each cylinder was covered with tightly stretched plastic wrapping material, to which spiders almost never attached their lines. After a web was built, we induced the spider to leave the web, removed the upper rim, coated the web on it lightly with talcum powder, and photographed it against a black background. We measured the lengths and areas and counted the web elements listed in Table 1 from digital photographs of webs using the NIH program "Image J" as in the previous study of *L. argyra* (Barrantes & Eberhard 2012).

Analyses of orb webs are facilitated by the large number of measurements that can be made on each web, but they are also challenging, because some variables may be correlated with each other only due to the regular geometry of the orb. We confronted this possible problem by measuring and reporting a wide variety of comparisons, but focusing on variables that are most likely to be independent of each other, especially on traits that are determined at different stages of orb construction (see discussion in Barrantes & Eberhard 2012).

To avoid measuring the same traits twice (Table 1), and to facilitate comparisons with the araneoid *Leucauge argyra*, we followed the conservative criteria for judging the independence and classification of different variables on the basis of their probable independence that were used by Barrantes & Eberhard (2012). The overall objective was to emphasize those web traits that resulted from different and thus possibly independent decisions made by the spider during construction and that could evolve independently. For instance, web design changes that were direct physical consequences of our manipulations were not counted: thus the association between reduced total area of the web and confinement in smaller spaces was not counted. Those stimuli and analyses of stimuli that spiders are unlikely to be able to perceive or to perform were also not counted. Thus we did not suppose that the spiders made any direct decisions regarding the number of loops of sticky spiral, as we judged that it was more likely that the number of loops was determined not by counting, but as

Table 1.—Relationship of total area of the web and 18 other web features, including the relationships between total area and the proportion of three features over the total area (each variable/total area) for webs built by *Zosis geniculata* spiders in containers with four different diameters, and comparison between slopes (t-test) of the same 18 variables for *Z. geniculata* and *Leucauge argyra*. *F*-test for the slope (H_0: b = 0), the slope values (b), standard error (SE) for slopes, and the proportion of the variance of each dependent variable explained by the total area (r^2) are included. All variables were log10-transformed. L indicates the longest radius, and areas are given as the square root of the actual values. Values of the t-test and probabilities are not presented for those features in which the slope did not differ statistically from zero in both *Z. geniculata* and *L. argyra*.

	Z. geniculata						*Z. geniculata* vs. *L. argyra*			
Variable	*F*	df	b	SE	r^2	*P*	b	SE	t-test	*P*
Total area (independent variable)										
Capture area	2836.0	1/117	2.29	0.043	0.96	<0.00001	1.39	0.029	17.23	<0.00001
Free zone area	270.3	1/117	1.15	0.070	0.70	<0.00001	0.68	0.048	5.54	<0.00001
Hub area	511.6	1/117	1.12	0.049	0.81	<0.00001	0.23	0.025	16.01	<0.00001
Number of radii	472.6	1/117	1.28	0.059	0.80	<0.00001	0.40	0.023	13.89	<0.00001
No. sticky spiral loops	135.6	1/117	1.77	0.147	0.54	<0.00001	0.89	0.044	6.24	<0.00001
Sticky spiral space on L	26.0	1/117	0.70	0.139	0.18	<0.00001	0.42	0.047	1.94	0.05297
Consistency st. sp. spaces on L	3.1	1/104	−0.07	0.040	0.03	0.0795	0.03	0.016		
Dist. from outer loop	83.4	1/116	3.49	0.382	0.42	<0.00001	1.04	0.123	6.12	<0.00001
Dist. longest radius	910.2	1/115	2.85	0.094	0.89	<0.00001	0.91	0.029	19.59	<0.00001
Dist. shortest radius	526.7	1/115	2.68	0.117	0.82	<0.00001	1.05	0.045	12.98	<0.00001
Web symmetry	0.25	1/115	0.02	0.036	0.002	0.618	0.44	0.065	5.68	<0.00001
Prop. radii attached to substrate	37.7	1/113	−0.27	0.044	0.25	<0.00001	−1.03	0.061	9.98	<0.00001
Prop. frame w. single radius	17.2	1/113	−0.21	0.050	0.13	0.00007	−0.46	0.068	2.28	0.02355
Mean radii/frame	120.9	1/113	0.82	0.074	0.52	<0.00001	0.43	0.028	4.93	<0.00001
Number of frame lines	39.08	1/116	0.73	0.117	0.25	<0.00001	0.41	0.077	2.31	0.02212
Prop. capture area/total area	1155.0	1/117	0.60	0.018	0.91	<0.00001	0.03	0.028	17.11	<0.00001
Prop. free zone area/total area	61.3	1/117	0.22	0.028	0.34	<0.00001	0.03	0.028	4.88	<0.00001
Prop. hub area/total area	149.6	1/117	0.24	0.020	0.56	<0.00001	−0.19	0.014	17.62	<0.00001

a result of a combination of decisions including how close to the end of the radius to attach the first loop, how far apart subsequent loops were attached, and where sticky spiral construction was terminated. We also took into account the physical feasibility of independence among variables. For instance, it is not physically possible for the total number of radii to be independent of the mean angle between them, so we only measured the number of radii (as an indicator of the angle).

Finally, we considered those variables that were directly affected by decisions that were made at different times during construction, and that are influenced by different cues, as likely to be biologically independent. It is important to note that biological independence is not necessarily the same as statistical independence. For instance, the two variables radius length and the distance from the end of the radius at which the first loop of sticky spiral is attached are correlated statistically (Barrantes & Eberhard 2012). But radius length is determined much earlier in orb construction than is the placement of the first loop of sticky spiral. Sticky spiral placement is influenced by the site of the outer loop of temporary spiral (Eberhard 1972, 2012), a line that is not even present when radii are being constructed. Thus despite their statistical correlation, we considered these two aspects of design to result from different decisions.

Measurements of spaces between loops of sticky spiral on the longest radius and the radius opposite it differed slightly from those described by Barrantes & Eberhard (2012) for *L. argyra*. As in other uloborids (Eberhard 1972; Lubin 1986), *Z. geniculata* does not attach the sticky spiral to each radius it encounters. When a loop of sticky spiral was not attached to a particular radius (determined by lack of an inflection in the sticky line, and by lack of reduction in the diameter of the line associated with the attachment – see Fig. 2b), we measured the inter-loop distance where that loop was attached to the nearest radius. In a few cases, the spacing was uncertain because sticky loops were broken or adhered to each other; in these cases we substituted a measurement of the inter-loop distance on an adjacent radius. We also measured the distance between the outermost loop of sticky spiral and the outer end of the radius (its attachment to a frame line or the wall of the container) for the longest radius and the radius opposite it.

In the behavioral descriptions we use the terms "inner" and "outer" with reference to the hub of the orb; thus the "outer" leg I (leg oI) is farther from the hub than leg iI as the spider circles the web. Similarly, we use the expressions "beyond" or "far side of" with reference to the direction the spider was moving, so a line "beyond" the radius a spider encountered while the circling the web was on the far side of that radius. To improve the clarity of descriptions, we refer to the spiders as "she" rather than "it" (in point of fact, all the spiders in our study were mature females).

Measurements of spaces between sticky spiral lines were standardized to control for differences in spider size, recent feeding history, and the general area of the web by standardizing data: eaeh measurement was divided by either the median space on that radius, or by the spaces just preceding or following an experimental space. It is likely that a spider's responses to cues at different sites in her web were largely independent of each other, but to account for the possible effects of including multiple measurements from the same web and using different webs of the same spider, we analyzed the data with general linear mixed models (GLMM).

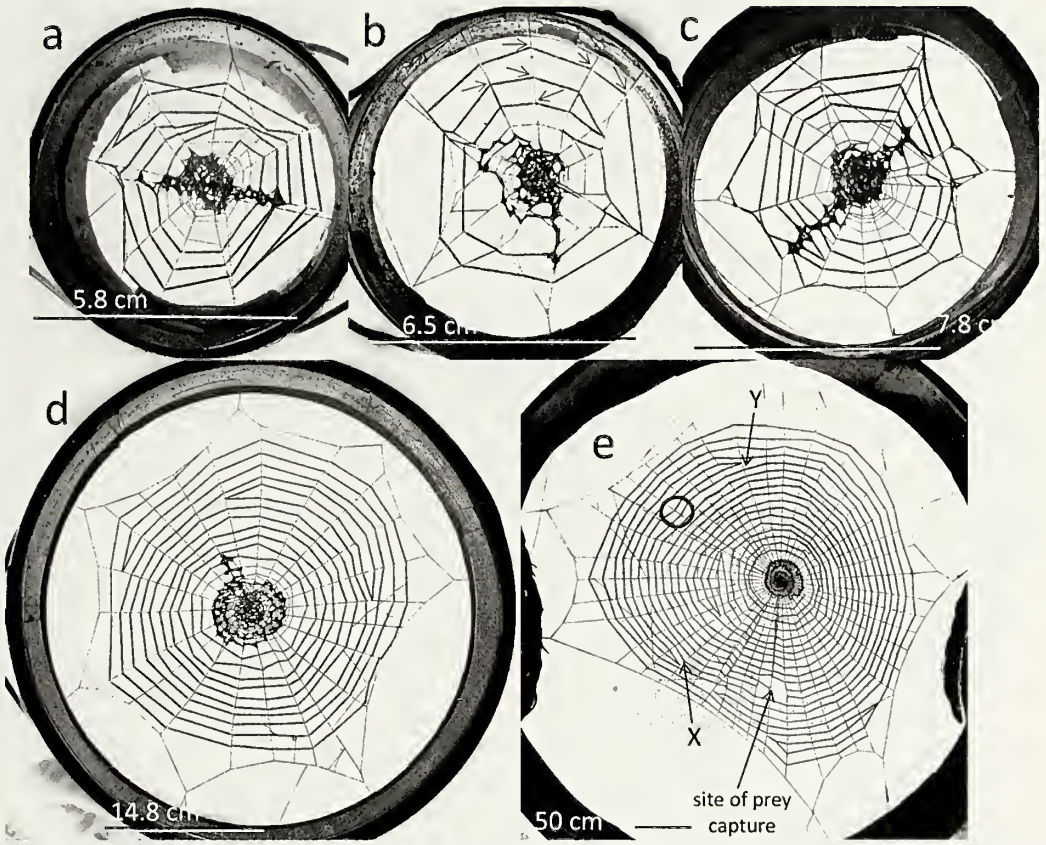
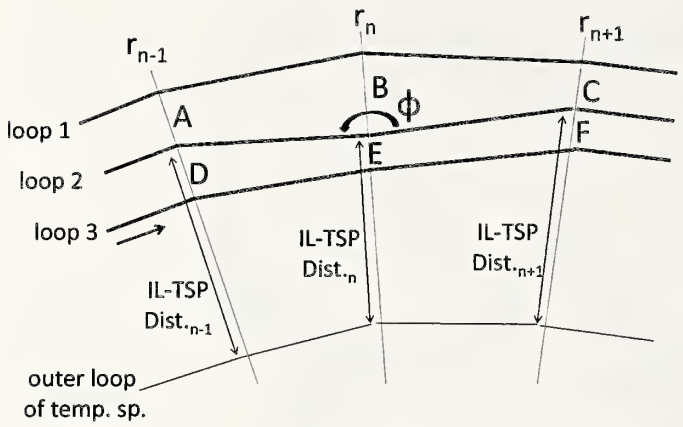


Figure 2.—Orbs built by the same mature female *Z. geniculata* in containers with different diameters: a) 5.8 cm; b) 6.5 cm; c) 7.8 cm; d) 14.8 cm; and e) 50 cm. The sticky spiral lines are slightly thicker than radii and frame lines because they have more powder on them. The arrows in b indicate asymmetries in the sticky line on either side of attachments to radii that reveal the direction in which the spider was circling the web (also indicated by the arrows); the sticky spiral line is thinner on the far side of the radius, probably because the spider did not comb out the first small segment of sticky cribellum lines immediately after making an attachment. The circle in e) indicates a site with a spontaneous inward deflection of the sticky spiral that offered an opportunity to test the effect of changes in the IL-TSP distance (see Figure 4). "X" indicates a spontaneous "Hingston experiment" at a turn back site, while "Y" indicates a "control" at another turn back site.

For instance, when we used experimental and unaltered control webs (fixed factors in the model) to test a possible effect but made multiple measurements of the same web, we nested measurements within webs and considered the web as a random factor within the GLMM. Most GLMM results are reported in the figures, to simplify the text. We used figures and regressions from linear models for illustrative and comparative purposes only after determining that the random factors included in GLMM had no significant effect using the Akaike information criterion (AIC). We used the R statistical Language (version 2.15.3: R Core Team 2013) for all statistical and graphical analyses.

Responses to naturally occurring deviations in the inner loop site cue.—During sticky spiral construction in unaltered webs, spiders were occasionally confronted with situations similar to that in a Hingston experiment (Fig. 1a). A naturally occurring deviation of this sort (corresponding to a "spontaneous Hingston experiment") occurred when the spider encountered a previous turn back site (Fig. 1b). Because direct observations showed that the spider's inner loop localization movements always involved tapping on the far side of the radius rather than on the near side (inset in Fig. 1b), we deduced that the spider had failed to contact the inner loop of the turn back at such a site when she was moving in the direction that she had been moving just prior to the turn back (inset in Fig. 1b). But when she moved in the opposite direction, she did contact the inner loop ("controls"). The direction the spider was moving when she encountered such a site was deduced using both the asymmetry of attachments to radii, and by tracing the path of the sticky spiral line. The spider's path during sticky spiral construction was traced in photographs of 50 webs built in large (50 cm dia) containers by 15 females (Fig. 2e). We did not count cases in which a spider did not attach the sticky spiral to the radius where the turn back occurred. We also excluded cases in which the spider turned back after attaching to the experimental radius (the one with the previous turn back) or to either of the two adjacent radii, because turn back spaces tended to be smaller. Sample sizes were slightly different for some comparisons due to these exclusions.

We tested whether *Z. geniculata* uses the reference point cue from the inner loop ("IL" site) as araneoid spiders do as follows. The sticky spiral attachment to radius r_n in Fig. 1b would be expected to be displaced outward compared with attachments to radii immediately preceding and following this radius (distance A would be smaller than distances B and C in Fig. 1b); in addition, the outward displacement (A) would be relatively smaller or absent in control encounters compared with the distances on adjacent radii (B, C). These tests were especially powerful because they involved within web



	Yes	No	Chi²	df	p
E < D	58	255	122.4	1	< 0.00001
E < F	59	253	120.6	1	< 0.00001
E < (D + F)/2	33	279	194.0	1	< 0.00001

Figure 3.—Schematic drawing of the distances measured on *Z. geniculata* webs to test whether spiders used the TSP-IL distance cue. At sites in the orbs in which the inner loop of sticky spiral veered inward for one attachment (angle φ at r_n was < 180°), the spacing of the next loop of sticky spiral on r_n (E) was compared with the spacing on the preceding radius (D on r_{n-1}) and on the following radius (F on r_{n+1}). For reasons of clarity, the subsequent loops of sticky spiral are omitted; possible IL-TSP distances are shown in the drawing even though they were not measureable in the webs because the temporary spiral lines were removed by the spider during sticky spiral construction. Although IL-TSP distances were not measured directly and thus presumably only differed as depicted in the drawing on average rather than in every case, the prediction that E would tend to be less than both D and F was fulfilled, as indicated by the GLMM values.

comparisons that held many spider and web variables essentially constant.

Responses to naturally occurring deviations in temporary spiral distances.—We used other natural deviations that occurred during the construction of unaltered orbs in 50 cm dia containers to test the hypothesis that *Z. geniculata* uses the IL-TSP distance cue to guide where to attach the sticky spiral to the radius in the same way that araneoid spiders do (Eberhard & Hesselberg 2012). As can be seen in Fig. 2e, the spaces between sticky spiral loops varied. In some cases a loop of sticky spiral was attached substantially farther from the inner loop on one radius than on the adjacent radii on either side (circle in Fig. 2e); in Fig. 3, distance B is greater than both A and C, and the angle φ on r_n is less than 180°. When the spider arrived at such a site on her next trip around the web (e.g., to attach loop 3 to r_n in Fig. 3), we assumed that the IL-TSP distance on r_n tended to be smaller than the IL-TSP distances on r_{n-1} or r_{n+1}. If the spiders were using changes in the IL-TSP distance as a cue for sticky spiral spacing as araneoids do (Eberhard & Hesselberg 2012), then the space for loop 3 on r_n (E in Fig. 3) was predicted to tend to be smaller than the spaces on the radii immediately preceding (E < D) and following (E < F). We tested this prediction by examining sites in which φ < 180°, and measured the distances A-F in Fig. 3. We again analyzed the data using GLMM and standardized values, so as to take into account the possible effects of multiple measurements on the same web and multiple webs of the same spiders.

Responses to naturally occurring deviations in the amount of sticky silk available.—Spiders sometimes took two nights to complete an orb, building all non-sticky lines and the outer portion of the sticky spiral on the first night, then finishing the sticky spiral on the second (Fig. 4). "Two-night" webs were built only in 50 cm diam containers, and never in smaller ones. If one makes the seemingly reasonable assumption that the eribellum glands fill only gradually rather than instantaneously with silk after sticky spiral silk is pulled from them (Witt et al. 1968), then on the second night the spider's cribellum glands were probably more full of silk when she resumed sticky spiral construction than they had been when she ended sticky spiral construction on the previous night. We thus used two-night webs to test the hypothesis that cribellum gland contents influence sticky spiral spacing. We marked the innermost loop of sticky spiral after the first night with small dots of talcum powder, and then photographed the web after the second night, when the spider had completed the sticky spiral (Fig. 4). We measured the spaces between all sticky spiral loops on the longest radius and on the radius most nearly opposite this radius.

Interruption of sticky spiral production occurred on the first night at different stages of sticky spiral construction: from 4 to 21 loops were built on the first night, and 5 to 19 on the second. We thus compared loops with respect to initiation and termination on a given night rather than with respect to the absolute numbers of loops. To combine data from different webs, and to control for the many variables that were not held constant and that may influence sticky spiral spacing (e.g., spider size, recent feeding experience, radius length, distance from the hub), we standardized all measurements of distances between loops by dividing each by the median spaee for that particular radius.

Effects of changes in radius tension on sticky spiral construction.—Several possible cues that a spider might use during sticky spiral construction are physically dependent on the tensions on the radii. These include resonant vibrations of lines, vibrations transmitted from other lines, and the tensions themselves. The possible use of such tension-related cues has been tested and found to be absent in araneids (Eberhard & Hesselberg 2012) and the uloborid *Uloborus diversus* Marx 1898 (Eberhard 1972) by experimentally breaking radii during sticky spiral construction. We replicated these experiments in "two-night" *Z. geniculata* webs in large (50 cm diameter) containers. Two groups of two or three radii were cut in the outer portion of the web with a scissors while the spider rested at the hub following the first night. After the spider finished the sticky spiral the second night, the web was coated and photographed (Fig. 5b). The spaces between loops that were attached to broken (lax) radii ("II" in Fig. 5) were compared with spaces between attachments to the intact radii on the near and far sides of the hole ("I" and "III" in Fig. 5), whose tension was more or less unchanged. The intra-web comparisons in these experiments again held several variables known to affect sticky spiral spacing constant or nearly constant.

Experimental reductions of the space available in which to build.—We altered the size but not the shape of the space available to the spiders in which to build their webs by housing them in different sized cylindrical or nearly cylindrical containers; the diameters at the upper end were 5.8 cm (a segment of

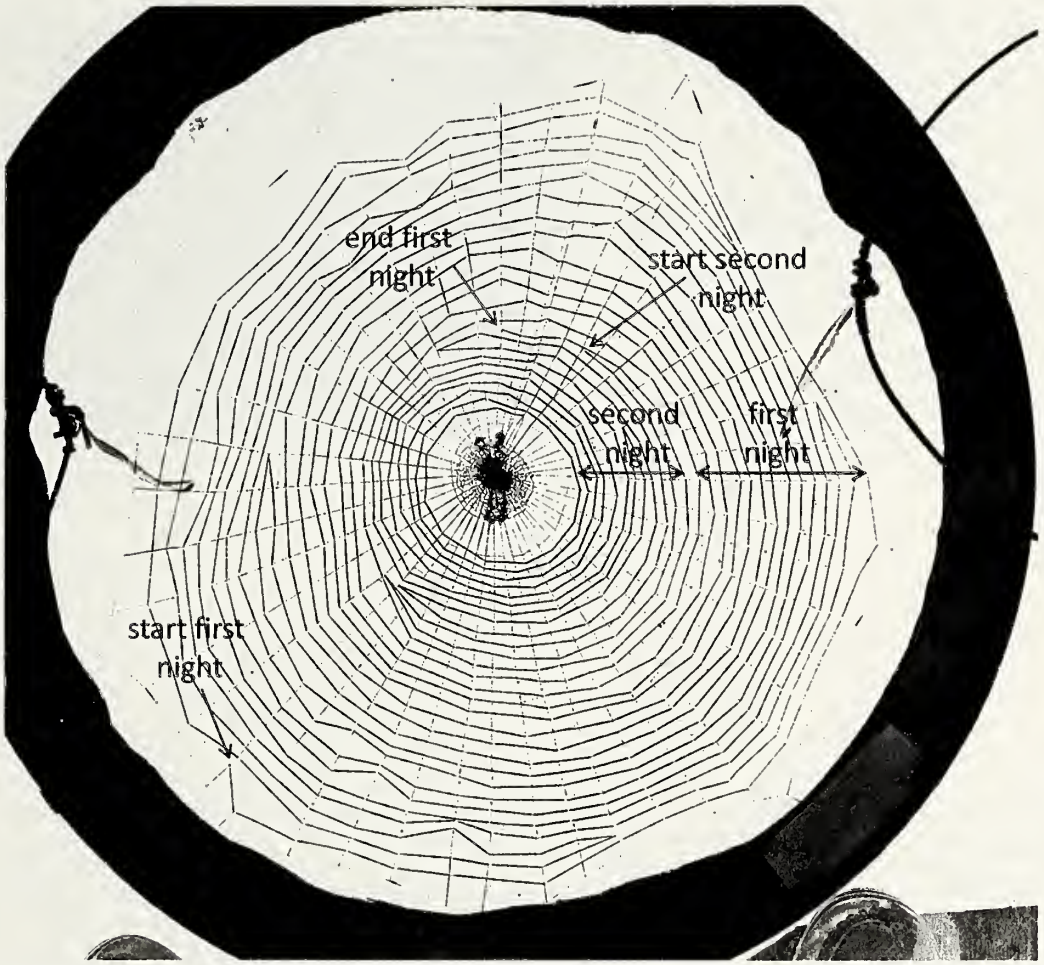


Figure 4.—A two-night web of *Z. geniculata*. On the first night, the hub, radii, and frame lines were all built and the spider laid the sticky spiral from the edge to the point indicated by the arrow "end first night" while moving counterclockwise. On the second night, she filled in the rest of the sticky spiral, beginning at "start second night" and moving clockwise.

PVC pipe), 6.5 cm (a section of a clear plastic soft drink bottle), 7.8 cm (a clear plastic cup for cold drinks), 14.8 cm (a white plastic half-gallon container), and 50 cm (a large plastic wash tub) (Fig. 2). The order in which an individual spider was housed in containers of different sizes varied randomly. Spiders generally built an orb within one or two days after being introduced into a container. We used the first web that a given female built in each size of container. Spiders were not fed until the end of the experiment. Nearly all females built a web in most or all of the different-sized containers, allowing for statistical comparisons in whieh spider identity was kept eonstant. In addition to the variables listed in Table 1, we measured the spaces between all adjacent loops of sticky spiral on the longest radius on which clear spaces were observable. The "span" of a web was the diameter of the container.

We caleulated the "consistency" of the distances between adjacent loops of sticky spiral using a modification of the technique of Eberhard (2007). The space between each loop of sticky spiral attached to a radius ("$space_n$") was compared with the space immediately previous and the space immediately following on the same radius by calculating the following ratio: $(space_n)/((space_{n-1} + space_{n+1})/2)$. Greater deviation of the value of this ratio from 1.0 indicated greater inconsistency. The symmetry of the web was quantified by dividing the length of the radius opposite the longest radius (distance from center of hub to frame line) by the length of longest radius of the orb (greater approximation to the maximum value 1.0 indicated greater symmetry). The total area of the web was estimated by measuring the area enclosed by the outermost loop of sticky spiral. All variables were $\log_{10}$ transformed to reduce deviation from a normal distribution, to facilitate statistical analyses; all means are followed by ± 1 standard deviation.

We were not able to directly judge the sizes of our containers in comparison with the sizes of the areas of unrepaired *Z. geniculata* orbs in the field, because all of the field webs that we found had repaired sectors. In captivity, repair sectors were often larger than the sectors that they replaced, and "repairing" an orb is apparently a mechanism that *Z. geniculata* spiders use to expand their original orbs. Field webs often spanned spaces that were larger than the 50 cm diameter of our largest cages, but 50 cm may nevertheless be close to the typical span of a single unrepaired orb in the field. In any case, it is clear that the orbs built in our 7.8, 6.5 and 5.8 cm diameter containers were all unnaturally small, and thus represent challenges similar to those posed for the araneoid *Leucauge argyra* in a previous study (Barrantes & Eberhard 2012).

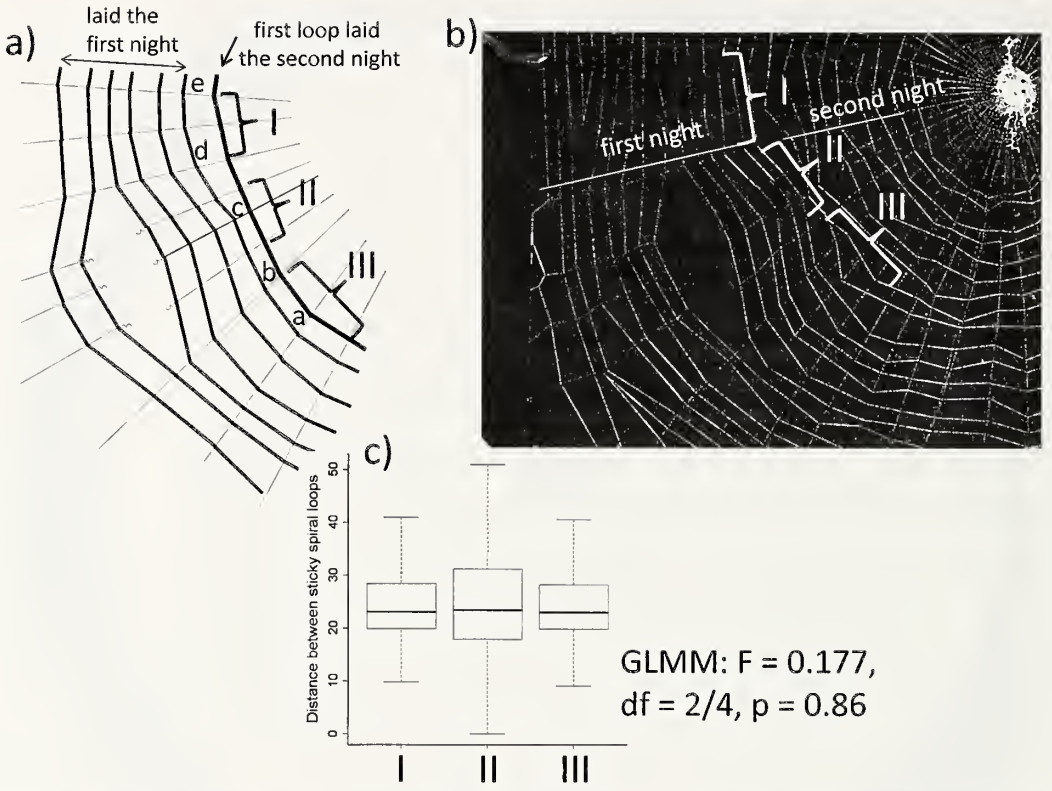


Figure 5.—a) Spaces that were measured in two-night webs that included three lax radii that were broken experimentally after the first night. The distances at which the first loop that was built the second night that crossed the three lax radii (II) and the unbroken radii that were encountered just before (I) and just following (III). b) A portion of a two-night web of a mature female of *Zosis geniculata* in which three radii were broken experimentally following the first night (arrows) and the spider then laid loops of sticky spiral on the second night. c) Results of the experiment: there was no effect of radius tension on the distance between loops of sticky spiral.

RESULTS

Naturally occurring deviations in the inner loop site cue.—We checked for the differences in the standardized distances between sticky spiral loops predicted by the monophyly hypothesis in 120 naturally occurring deviations in the inner loop site cue and 101 control encounters in 49 webs of 13 *Z. geniculata* spiders (Fig. 6). In such "Hingston experiment equivalents", the "experimental distance" (A in Fig. 1b) showed consistent trends to be less than the distance on the previous radius (B) in 76.7% of 120 cases, and less than that on the radius immediately following (C) in 77.4% of 106 cases (Fig. 6a, c). Corresponding values for control situations were 46.5% and 48.7%, and the results of the GLMM (Fig. 6b, d) indicated slightly opposite intra-web trends for control situations. Comparisons of central values for experimental and control situations showed similar trends. The mean value of A was significantly smaller than the mean of B and C in Hingston experiments, but not in controls (Fig. 6a–d). In sum, the sticky spiral of *Z. geniculata* tended to be displaced outward, away from the hub when these naturally occurring deviations in the inner loop site occurred.

A second clear trend was that the size of this outward displacement of the sticky line fell short of that which would have been expected if the spider were using only the inner loop site cue. Instead of A being 0 (as in Fig. 1a), T+A was significantly greater than B or C (Fig. 6e, f). This trend was also predicted by the monophyly hypothesis, because this same trend also occurs in araneoids (Eberhard & Hesselberg 2012). This trend is compatible with the hypothesis that the temporary spiral distance is an additional cue that has a negative correlation with the space between loops. This is because the tendency of the temporary distance on r_n to be greater than those on r_{n-1} or r_{n+1} (see Fig. 1b) would result in T+A being larger than B or C, as was indeed found to occur.

Natural deviations in temporary spiral distance.—We made a second test of the hypothesis that the temporary spiral distance influences sticky spiral spacing in *Z. geniculata* by checking for the predicted differences in spaces in 946 cases in which φ_n was $< 180^\circ$ (circle in Figs. 2e, 3) in 80 unaltered orbs built by 11 spiders. The predictions were again confirmed. The spacing of the loop of sticky spiral built when the spider had experienced a shorter temporary spiral distance (E in Fig. 3) tended to be smaller than the spacing on the radii immediately preceding (D) and following (F) (Fig. 7). In addition, there was a positive correlation between φ on r_n (Fig. 3) and the reduction in the standardized space on that radius (E in Fig. 3) when it was compared with the mean of the standardized spaces on the previous and the following radii (E/(D + F)/2) (Fig. 8).

Effects of probable changes in cribellum gland contents.—The median standardized spaces between sticky spiral loops at different stages of sticky spiral construction in one and two-night webs are shown in Fig. 9. Comparisons were complicated by the fact that, as in many araneoids (e.g., Peters 1939; LeGuelte 1966; Herberstein & Heiling 1999; Eberhard 2013),

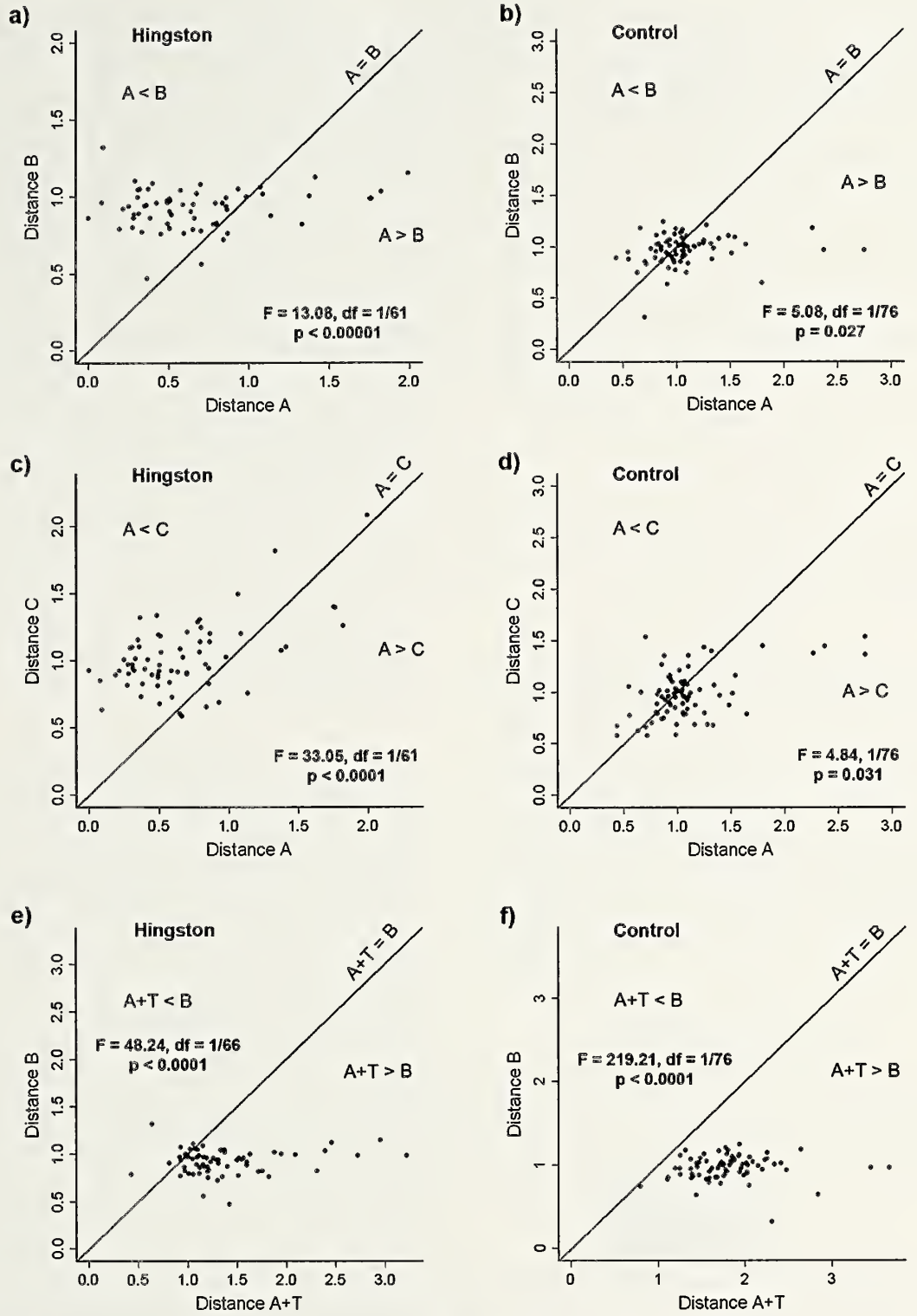


Figure 6.—Within-web comparisons of the results of spontaneous Hingston experiments and controls (letters as in Figure 1b); the line in each graph represents lack of an effect, and each dot represents a situation like that in Figure 1b in which two distances are compared. As predicted if the spider is guided by the IL site cue, the experimental space tended to be smaller than the space immediately preceding it (A <B) in experiments ("Hingston") (a) than in controls ("Control") (b), and also than that immediately following it (A <C) in experiments (c) but not controls (d). Contrary to the prediction if only the IL site cue is used, however, the sum of A+T tended to be greater than the preceding space (A+T> B) in both experiments (e) and controls (f). This difference is in accord with the hypothesis that an additional cue (the TSP-IL distance; see Figure 3) is also used. The GLMM comparisons of the corresponding distances are indicated by *F* values.

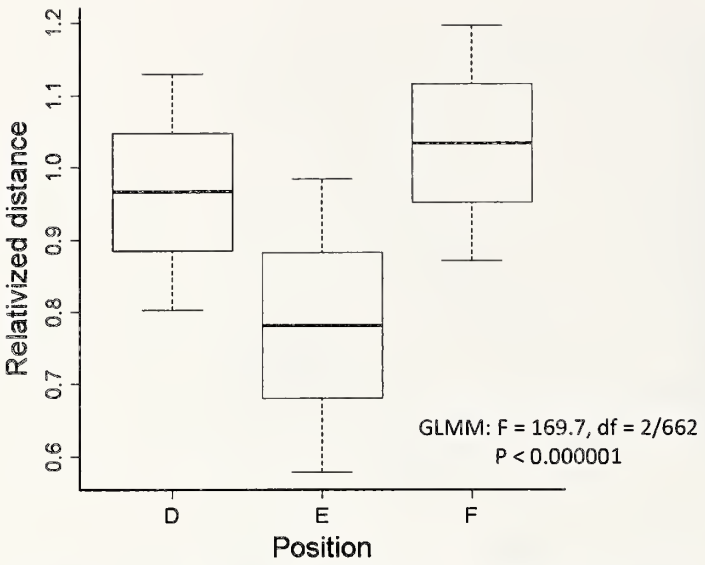


Figure 7.—There was a reduction in the standardized distance between adjacent loops of sticky spiral at a point where the inner loop of sticky spiral bent inward (E) compared with the distances of the attachments immediately preceding and following (D, F) (see Figure 3), as indicated by the GLMM analysis.

the spaces between loops of sticky spiral decreased gradually from the edge of the web toward the hub (e.g., one-night webs in Fig. 9c, d). There were two trends in two-night webs (Fig. 9a, b) that are compatible with the prediction of the monophyly hypothesis that sticky spiral spacing has a negative correlation with the amount of silk available in her cribellum glands in *Z. geniculata*. The spaces between the last two loops of sticky spiral that the spider laid on the first night (when her supplies of cribellum silk may have been running low) were especially large. In addition (and more importantly), the first loops that she laid at immediately adjacent sites on the same radii on the second night (when her silk supplies were likely

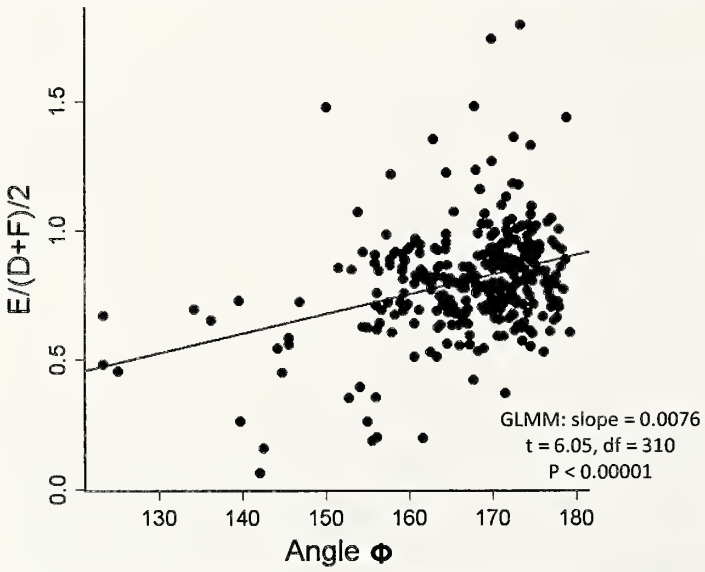


Figure 8.—There was a positive correlation between the angle at which the inner loop veered inward (angle ϕ in Figure 4) and the reduction in the standardized sticky spiral spacing (E/(D+F)/2), as indicated by the GLMM values.

more complete) were sharply smaller on both the longest radius (GLMM: $F = 2.77$, df = 1/13, $P < 0.001$) and on the opposite radius (GLMM: $F = 5.49$, df = 1/13, $P < 0.0001$) (Fig. 9a, b).

Altered tensions on radii.—The spaces between successive loops of sticky spiral attached to a lax radius which had been broken were neither consistently larger nor smaller than the preceding two spaces on intact radii nor the next two on the following intact radii (Fig. 5c). These comparisons again held constant or nearly constant several variables (spider size, distance from the hub, silk supplies) that probably influence sticky spiral spacing.

Effects of space available in which to build.—Reduced space in which to build affected multiple aspects of orb designs in *Z. geniculata* webs (Figs. 2, 10, Table 1). These effects were not affected by including several webs of the same spider in the GLMM models (Table 2). These effects were strikingly similar to those of similar experiments with the araneoid *L. argyra* (Barrantes & Eberhard 2012) (Fig. 10, Table 1). All of the seven variables that are likely to be under independent behavioral control (using possibly overly-conservative criteria to judge independence; see Methods, Barrantes & Eberhard 2012) showed similar changes in the two species when total web area changed, as predicted by the monophyly hypothesis. With the exception of two variables (web symmetry and consistency of spacing), the slopes were higher in *Z. geniculata*.

DISCUSSION

Tables 3 and 4 summarize the comparisons between cues guiding orb construction in uloborids and araneoids and the types of data on which they are based. The two groups are clearly similar. We obviously cannot claim to have documented the full diversity of cues and responses in either group. But the existence of substantial similarities confirms the prediction of the monophyly hypothesis. Within the limitations of the statistical analyses (it is not possible to disprove a null hypothesis of lack of difference, but only to demonstrate that it is improbable), the differences in the stimuli and responses to them in the two groups predicted by the polyphyly hypothesis did not occur. We discuss detailed comparisons below.

Reference stimuli that guide sticky spiral placement.—*Inner loop site and temporary spiral distance cues*: The uloborid *Z. geniculata* resembles araneoids both in sensing IL site and TSP-IL distance cues, and in responding to these cues in a similar manner. Thus *Z. geniculata* resembles the araneoids in sensing the IL site, and in responding to an outward displacement of this site by displacing the attachment of her sticky spiral outward. The attachment of the sticky line to the radius was displaced outward in the naturally occurring deviations in the inner loop cue (the "spontaneous Hingston experiments") in *Z. geniculata*, just as occurs in all four araneoids that have been tested (Hingston 1920; Peters 1954; Eberhard & Hesselberg 2012). These cues are available to the spiders because, as in araneids, uloborid spiders use leg of to locate the IL site (Eberhard 1982).

In addition, the outward deflection in "spontaneous Hingston experiments" was less than would have been predicted if the IL site were the only reference stimulus (as

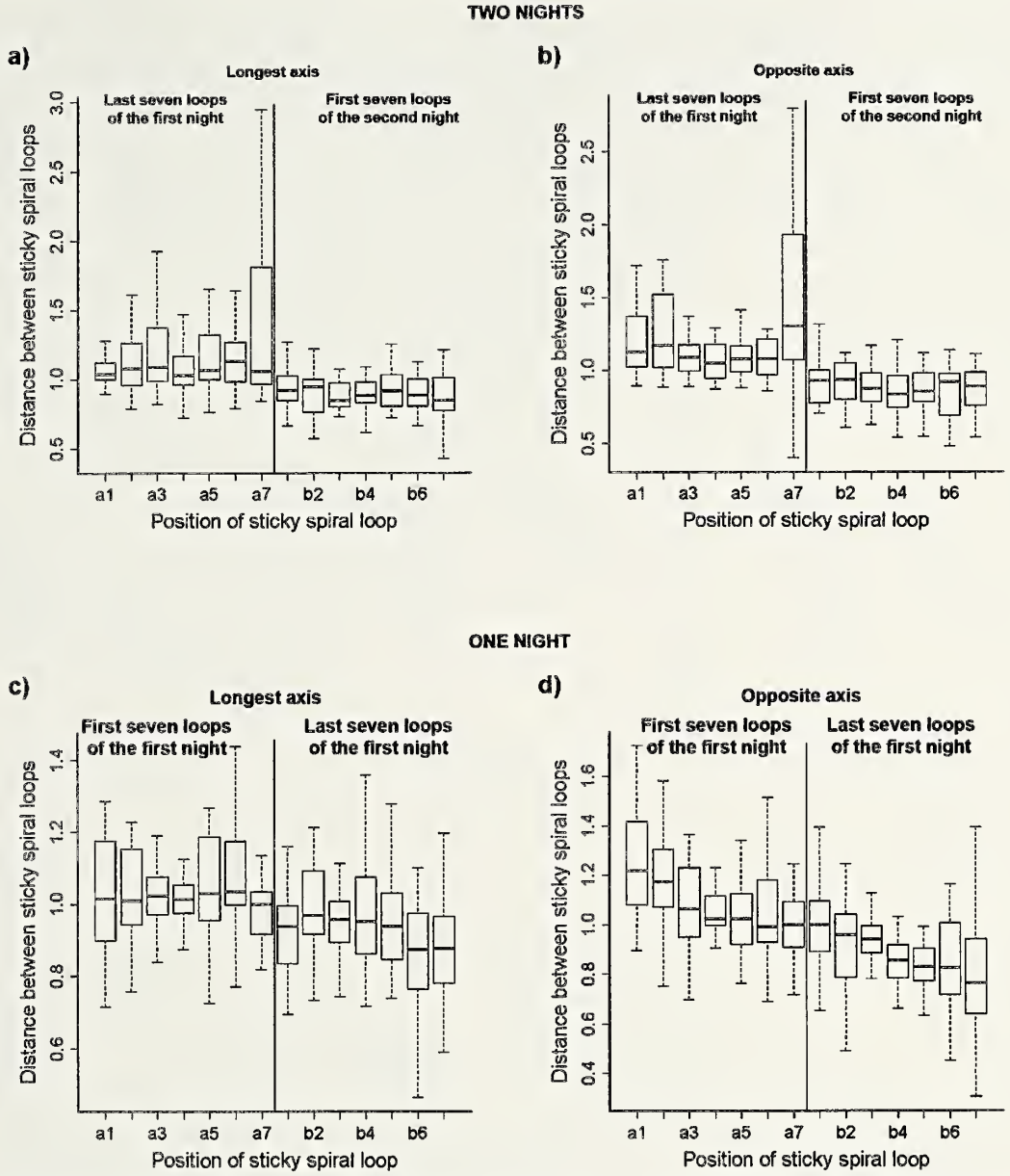


Figure 9.—The distances (medians, quartiles and ranges) of the standardized spaces between successive sticky spiral loops in orbs built by *Z. geniculata* over two nights (above) decreased abruptly in the first seven loops of the second night, both on the longest radius and the opposite radius. In webs built in a single night (below), the means decreased gradually along the entire length of each of these two radii. Measurements from different single night orbs that had different total numbers of sticky spiral loops are combined by plotting the first seven (a1 to a7) and the last seven spaces (b1 to b7) in each web (all measurements in both two-night and one-night webs were standardized by dividing by the median value for the entire radius).

was supposed by Hingston 1920). These "incomplete" responses to inner loop site cues, which are probably due to the use of a second, TSP-IL distance cue (Eberhard & Hesselberg 2012), were very similar to those observed in the araneoids *M. duodecimspinosa* (O. P.-Cambridge 1890) and *L. mariana* (Taczanowski 1881) (and may have also occurred in *Neoscona nautica*) (Eberhard & Hesselberg 2012).

The hypothesis that *Z. geniculata* uses the TSP-IL cue was also supported by a second pattern in their webs. When the inner loop on one radius was displaced inward substantially with respect to attachments on adjacent radii (B compared with A and C in Fig. 3), the spacing of the next loop of sticky spiral (E) tended to be reduced. The same pattern of "compensatory" spacing occurs in the orbs of the araneoids *M. duodecimspinosa, L. mariana* and *Allocyclosa bifurcata* (McCook 1887) (Eberhard 2011; Eberhard & Hesselberg 2012). It probably results from their also using the TSP-IL distance to guide sticky spiral placement (Eberhard & Hesselberg 2012).

Still another indication that both uloborids and araneoids use the site of the outer loop of temporary spiral in determining attachment sites of the sticky spiral comes from observations of the placement of the first, outermost loop of sticky spiral. In the uloborid *U. diversus* (Eberhard 1972) and

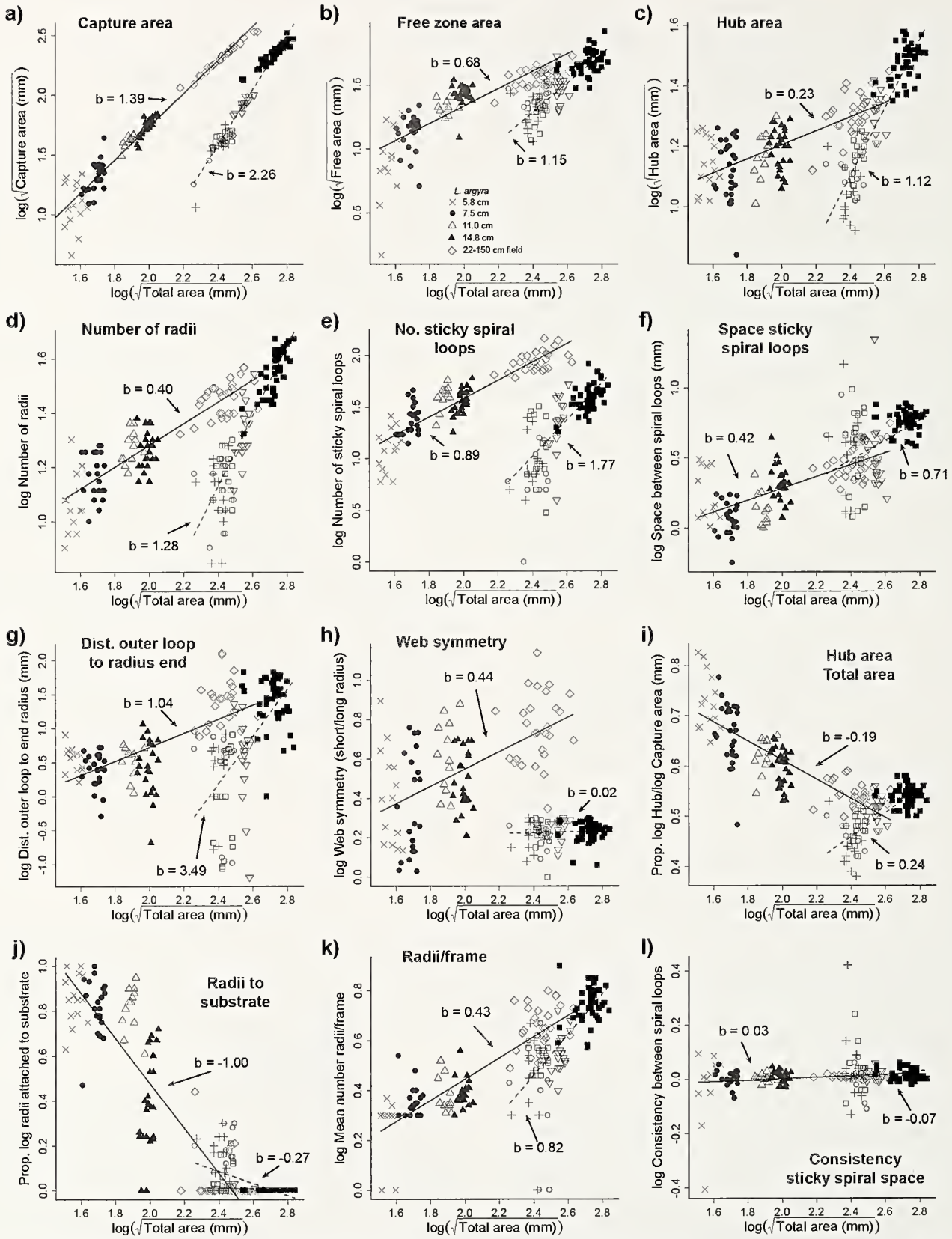


Figure 10.—Relationships between different aspects of web design and the total area of webs of *Z. geniculata* (solid line) and of the larger tetragnathid *L. argyra* (dotted line) (from Barrantes & Eberhard 2012) that were built in containers with different diameters (most were smaller than the sizes of the normal orbs of that species). The absolute values of slopes varied between species, but their signs and even the degree of dispersion around the regression lines were similar in most cases.

Table 2.—Results of the mixed effects models for 18 web features of *Zosis geniculata* (dependent variables). The total area of the web was in all cases the predictor variable. In one model, individual spiders were included as a random factor (model with random effects); in a second model, individual spiders were not considered as a random effect. Results obtained with both models were very similar as indicated by the values of the Akaike Information Criterion (AIC) included for both models. The asterisks indicate the significance associated to the effect of the intercept or the slope on each dependent variable: * $P < 0.05$, ** $P < 0.001$, *** $P < 0.0001$. All variables were log10−transformed. L indicates longest radius and areas are given as the square root of the actual values.

	Model with random effects (1)				Model without random effects (2)					
	Intercept		Slope (total area)		Intercept		Slope (total area)			
Variable	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	$AIC_{(1)}$	$AIC_{(2)}$
Capture area	−3.92***	0.112	2.29***	0.043	−3.92***	0.112	2.29***	0.044	−274.3	−276.26
Free zone	−1.48***	0.182	1.15***	0.071	−1.48***	0.182	1.15***	0.071	−161.71	−163.71
Hub area	−1.58***	0.129	1.12***	0.05	−1.57***	0.129	1.12***	0.05	−242.92	−244.92
Number of radii	−1.94***	0.15	1.28***	0.058	−1.93***	0.153	1.28***	0.06	−202.59	−203.78
No. sticky spiral loops	−3.36***	0.429	1.72***	0.162	−3.44***	0.384	1.74***	0.149	1.24	6.75
Sticky spiral spaces L	−1.23**	0.361	0.71***	0.141	−1.22**	0.362	0.71***	0.141	−2.45	−4.44
Consistency L	0.21	0.135	−0.08	0.05	0.2	0.105	−0.07	0.04	−278.82	−280.72
Dist. from outer loop	−8.19***	0.982	3.49***	0.382	−8.18***	0.982	3.49***	0.382	228.79	226.79
Length longest radius	−5.73***	0.236	2.85***	0.091	−5.70***	0.242	2.85***	0.094	−98.26	−99.05
Length shortest radius	−5.48***	0.276	2.71***	0.107	−5.41***	0.3	2.67***	0.117	−52.54	−48.36
Web symmetry	0.18	0.092	0.02	0.036	0.18*	0.092	0.02	0.036	−320.32	−322.32
Prop. radii attached to substrate	0.71***	0.13	−0.26***	0.05	0.73***	0.114	−0.27***	0.044	−273.56	−268.35
Prop. frame w. single radius	0.56**	0.142	−0.20***	0.054	0.58**	0.128	−0.21***	0.05	−243.13	−242.49
Mean radii/frame	−1.48***	0.211	0.81***	0.081	−1.50***	0.191	0.82***	0.074	−154.61	−153.32
Number of frame lines	−1.03**	0.301	0.73***	0.117	−1.03***	0.301	0.73***	0.117	−45.44	−47.44
Prop. capture area/ total area	−0.77***	0.046	0.60***	0.018	0.77***	0.046	0.60***	0.018	−481.74	−483.74
Prop. free zone area/ total area	0.01	0.073	0.22***	0.028	0.01	0.073	0.22***	0.029	−372.86	−374.86
Prop. hub area/total area	−0.12*	0.05	0.24***	0.019	−0.12*	0.051	0.24***	0.02	−456.44	−458.43

in the araneids *Araneus diadematus* Clerck 1757 (Zschokke 1993) and *M. duodecimspinosa* (Eberhard 2012) the location of the first loop of sticky spiral is correlated with the position of the outermost loop of temporary spiral.

In sum, the uloborid shows a detailed similarity with araneoids regarding use of and responses to two different reference stimuli during sticky spiral construction.

Tensions on radii: Neither the two uloborids, *Uloborus diversus* (Eberhard 1972) and *Z. geniculata*, nor the araneoids, *L. mariana*, *M. duodecimspinosa* (Eberhard & Hesselberg 2012), showed any changes in sticky spiral spacing in response to sharp experimental reductions in radius tension. The implication is that many alternative, tension-dependent cues that could be used to guide sticky spiral placement (e.g., resonant vibrations of radii, vibrations of other lines, resistance when pulled, and tensions) are not used in either the uloborid or in araneoids, supporting the monophyly hypothesis.

General settings stimuli that guide sticky spiral placement.—*Amount of sticky silk available*: The spiders in both groups sense the amount of silk present in sticky silk glands (cribellum and pseudoflagelliform glands in uloborids, aggregate and flagelliform glands in araneoids), and they increase the stieky spiral spacing when they have less silk available. The spaces between loops of sticky spiral in the two-night webs of *Z. geniculata* correlated negatively with the amount of sticky silk thought to be available to the spiders in their silk glands, and these resemble similar negative correlations in araneoids (Eberhard 1988b). Direct experimental manipulation of gland contents has not been performed in either group, however, so correlations with other stimuli might be involved. In sum, as far as the experiments go, the resemblance in the two groups supports the monophyly hypothesis.

Reduced spaces in which to build.—When the spiders were experimentally confined in small spaces of different sizes, there was a striking similarity between the several responses of *Z. geniculata* and those of the araneoid *L. argyra* (Fig. 10, Table 1). Of the 12 relations to total area in Fig. 10, ten are quite similar. The specific cues that triggered these responses are not known in either species, so the possibility that some similarities in the graphs are due to the use of different cues cannot be eliminated. Nevertheless, as far as the experiments go, these similarities are again in accord with the monophyly hypothesis.

It is probable that some of the responses illustrated in Fig. 10 are correlated and not independent of each other, so the number of valid comparisons is probably lower than suggested in the figure. Using the common sense criteria for independence proposed by Barrantes & Eberhard (2012) (see

Table 3.—Comparisons of the polarities of changes in webs built in more constrained spaces (e.g., smaller containers) by *Zosis geniculata* (Uloboridae), and by *Leucauge argyra* (Tetragnathidae) (data from Barrantes & Eberhard 2012). Changes that can be attributed to simple physical limitations imposed by smaller available spaces, and are not appropriately considered to be due to decisions by the spiders are marked with "*". Variables that are likely to reflect independent decisions by the spider (using conservative criteria—see methods and Barrantes & Eberhard 2012) are preceded by different letters. Some variables, whose cause and effect relations with respect to cues and responses may be more complex, are not labeled.

	Z. geniculata	*L. argyra*
Radii, frames, anchor lines		
A Number of frame lines	smaller[1,2]	smaller[1,2]
A Proportion of radii attached directly to the substrate	greater	greater
A Proportion of frame lines with only a single radius	greater	greater
A Number of radii/frame line	smaller	smaller
A Proportion of radii that end on "V" frame lines	greater[2]	greater[2]
B Number of radii	smaller	smaller
* Length of radii	smaller	smaller
Relative areas		
*Capture area	smaller	smaller
C Hub area	smaller	smaller
D Symmetry	?	greater
E Free zone area	smaller?*	smaller
Free zone area/total area	greater	greater
Hub area/total area	greater	greater
Hub		
C Number loops hub spiral	?[3]	no change[2]
C Space between hub loops	?[4]	
Circular stabilimentum loops	less frequent	–[5]
Sticky spiral		
F Space between loops of sticky spiral on longest radius	smaller	smaller
G Distance from outer loop of sticky spiral to end of radius	smaller	smaller
Number of loops of sticky spiral	smaller	smaller
E Distance from outer loop of hub to inner loop of sticky spiral (free zone)	smaller[2]	smaller[2]
Consistency of sticky spiral spacing on longest radius	no change	no change

[1] In both species, the positive relationship with total web area was only significant in the four smallest containers, and in the largest space the number of frames did not increase.
[2] Unpublished data, G. Barrantes & W. Eberhard.
[3] Inner portions of hub could not be distinguished due to the stabilimentum.
[4] Outermost loops only (inner loops were not generally distinguishable).
[5] No stabilimentum built in this species.

Methods), there were seven different types of responses to small spaces (Tables 1, 3); the two groups resemble eaeh other in all of them.

The most striking uloborid-araneoid difference in Fig. 10 is the positive relationship between the proportion of the area occupied by the hub to the total area in *Z. geniculata* (Fig. 10i), as compared with the negative relationship between these variables in *L. argyra*; at the same time, the absolute value of hub area was smaller in smaller webs in both species (Fig. 10c). The differencc may be related to the "launching platform" function of the hub for attacks on prey (Briceño & Eberhard 2011). The diameters of the hubs of normal webs are substantially greater than the length of the spider in *Z. geniculata*, but are substantially less than the length of the spider in *L. argyra* (counting her legs). Thus in *Z. geniculata*, proportionally larger reductions in hub area are feasible that will still leave the hub large enough for the spider to turn and find lines to grasp with her legs III and IV which support her during an attack (Briceño & Eberhard 2011).

One response to small spaces (reduced web symmetry in smaller spaces) oecurred only in *L. argyra* but not *Z. geniculata* (Fig. 11h). Web symmetry is determined early in orb construction, when the location of the hub is first established (Eberhard 1990; Vollrath 1992), but the cue (or cues) used by spiders at this stage that determine the site of the hub are very poorly known.

Other comparisons.—The spaces between sticky spiral lines are larger near the edge of typical one-night orbs of *Z. geniculata* than near the hub (Figs. 4, 9). Similar patterns in sticky spiral spacing occur in the webs of many araneoids (LeGuelte 1966; Herberstein & Heiling 1999; Eberhard 2013). The specific cue (or cues) used by the spider to sense her position on the web with respect to the hub is not known in either uloborids or araneoids, but the similarity in the trends also favors the monophyly hypothesis.

One trend documented in the space manipulation experiments with both *Z. geniculata* and *L. argyra* (A in Table 3) also extends to the normal webs of species in other araneoid families that build in very small spaces in the leaf litter, or have secondarily lost their orbs. Frame lines are less common and have fewer radii attached to them in the anapid *Anapisona simoni* Gertsch 1941 (Eberhard 2007, 2011) and the araneid *Paraneus cyrtoscapus* (Pocock 1898) in webs built in deep grass (Edmunds 1978), and are completely lacking or reduced to very short lines bearing only a single radius in the webs of the anapids *Comaroma simoni* Bertkau 1889 (Kropf 1990) and *Conoculus lyugadinus* Komatsu 1940 (Shinkai & Shinkai 1988), and the mysmenid *Trogloneta granulum* Simon 1922 (Hajer 2000; Hajer & Řeháková 2003). The responses of *L. argyra* and *Z. geniculata* to experimental reductions in available space thus resemble evolutionary responses to similarly reduced spaces in other araneoid groups, emphasizing the apparent generality of this response throughout araneoid orb weavers.

Diversity within araneoids.—The variation among araneoids with respect to some of the cues and responses employed in orb construction was greater than the minor differences in uloborid-araneoid comparisons. Araneoids loeate the site of the inner loop of sticky spiral during sticky spiral construction in a variety of ways: nephilids and a few araneids use leg oIV; and tetragnathids use leg iI (Eberhard 1982; Kuntner et al. 2008). On the other hand, most araneids and all uloborids use leg oI (e.g., Fig. 1b inset). The responses to the IL site as a reference cue that are shared by araneoids and uloborids have apparently been secondarily lost in some araneoids, including those in the derived araneoid families Theridiosomatidae, Anapidae, Symphytognathidae, and Mysmenidae (Eberhard 1982, 1987). Compensatory alterations in sticky spiral spacing in finished webs suggest that these derived families instead rely entirely on the temporary spiral distance

Table 4.—A summary of the stimuli and the responses to these stimuli that guide orb construction behavior in uloborid orb weavers as compared with araneoid orb weavers. "–" indicates there is no evidence for or against; "A" indicates evidence from araneoids, "U" indicates evidence from uloborids; "stsp" = sticky spiral.

				Type of evidence			References	
Cue used by araneoids	Response to cue by araneoids	Same cue used by uloborids?	Same response to this cue by uloborids?	Observed details of behavior	Patterns finished webs	Experimental modifications	Araneoids	Uloborids
Site where previous inner loop stsp crosses radius	used as pt. of reference for stsp spacing	Probably yes	Yes	A, U	U	A, U[1]	Hingston 1920, Peters 1954, Eberhard 1982	Eberhard 1972, 1982, this study
TS-IL distance during stsp const.	larger induces larger space between loops of stsp.	Yes?[2]	Probably yes[2]	–	A, U	–	Eberhard & Hesselberg 2012	this study
Amount of sticky silk available in glands	smaller amount induces larger spaces between loops of sticky spiral	Possibly yes[3]	Yes	–	U	A	Eberhard 1988	this study
Low tension of radii	no response in stsp spacing	Yes (not used)	Yes (lack of response)	–	–	A, U	Eberhard & Hesselberg 2012	this study
Smaller space in which to build[4]	reduce stsp spacing	Yes[4]?	Yes	–	A, U	A, U	Barrantes & Eberhard 2012, Hesselberg 2013	this study
Smaller space in which to build[4]	reduce number of radii	Yes[4]?	Yes	–	A, U	A, U	Barrantes & Eberhard 2012, Hesselberg 2013	this study
Smaller space in which to build[4]	reduce number frame lines, num. r/frame, increase num. r without a frame	Yes[4]?	Yes (all responses)	–	A, U	A, U	Barrantes & Eberhard 2012	this study
Smaller space in which to build[4]	relatively larger hub, fewer hub loops	Yes[4]?	Yes[5]	–	A, U[5]	A, U[5]	Barrantes & Eberhard 2012	this study
Smaller space in which to build[4]	outer loop placed nearer frame line (or beyond)	Yes[4]?	Yes	–	–	A, U	Barrantes & Eberhard 2012	this study
Smaller space in which to build[4]	reduce relative size free zone	Yes[4]?	Yes	–	–	A, U	Barrantes & Eberhard 2012	this study
Smaller space in which to build[4]	reduce symm. of orb	No[4]?	No change symm.	–	–	A, U	Barrantes & Eberhard 2012	this study
Edge vs. center area (distance from hub)	stsp spacing varies predictably	?[6]	Yes	–	A, U	–	Peters 1939, LeGuelte 1966, Eberhard 2012, 2014	Eberhard 1972, 2014, this study

[1] Conclusion is tentative due to small sample size.

[2] The rarity of complete responses in spontaneous "Hingston experiments" and the "compensatory" changes in sticky spiral spacing in *Z. geniculata* are both compatible with the spider also using the TSP-IL distance as a cue to guide sticky spiral spacing, as has indeed been shown to occur in the araneoids *Micrathena duodecimspinosa* and *Leucauge mariana* (Eberhard & Hesselberg 2012).

[3] Both the increased spacing of sticky spiral loops just prior to spontaneous interruption of the sticky spiral, and the sharply reduced spacing when construction was resumed the following night in *Z. geniculata* are compatible with the hypothesis that sticky spiral spacing is influenced by the amount of silk available in the spiderã s cribellum glands.

[4] The specific cue (or cues) used are not known in either araneoids or uloborids. All data are from finished webs built under experimental conditions. The reasons for considering the 7 different responses to small spaces that are listed here as being biologically independent are discussed in the text and in Barrantes & Eberhard 2012.

[5] Data on relative hub size are available; but no data are available on number of hub loops for uloborids. In any case, all hub loops in uloborid webs are built during radius construction (in contrast with many araneoids – Eberhard 1990), so the number of loops may not be biologically independent of radius number in uloborids.

[6] The cue (or cues) are not known in either araneoids and uloborids.

cue (or the distance from the hub in the groups in which there is no temporary spiral) (Eberhard 2011).

In sum, the cues that guide sticky spiral placement show as much or more diversity within araneoids as they do when comparing araneoids with uloborids. This emphasizes the strength of the support for the orb web monophyly hypothesis.

Implications for phylogenies.—Recent molecular studies (Fernández et al. 2014, Bond et al. 2014) suggested that there are two likely alternatives: the orb web either evolved earlier than previously hypothesized, and is ancestral for a majority of spiders, including those in the RTA clade; or else it had multiple, independent origins, as was hypothesized by precladistic authors. The behavioral characters examined in the present study support the first of these alternatives.

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Movement, sex ratio, and population density in a dwarf male spider species, *Misumenoides formosipes* (Araneae: Thomisidae)

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Abstract. Crab spiders in the subfamily Thomisinae rank among the most extreme animals in terms of sexual size dimorphism (SSD). Hypotheses regarding the apparent selection for dwarfing of males relative to females generally reference advantages of small male size for mobility. Specific proposals claim that selection should be strongest in species with limited male-male combat, which would otherwise favor larger males. We aimed to determine if the predicted traits of low densities, female biased sex ratios, more movement by males, and limited male-male conflict characterized a population of *Misumenoides formosipes* Walckenaer 1837. New and previous assessments of these characteristics in this extremely dimorphic spider revealed a mix of support and discordance with the predicted set of traits. Repeated plot censuses over 2 years, together with daily monitoring of females and collections of males, documented relatively low densities with males outnumbering females by as much as 2.37:1. The movements of marked males were measured upon rediscovery during daily searches using two methods: tracking individuals from their point of discovery and trials in which males were moved to predetermined positions relative to females. Female movements were measured by marking their hunting positions followed by daily searches of these locations. Female average tenure across their locations was twice that of males (5.05 versus 2.45 days) and the initial moves made by marked males in trials were six times further than initial moves by monitored females (1.76 versus 0.29 m). Male-male conflicts over positions near females are frequent and intense in *M. formosipes*. By contrast, male fights are rare in the female biased populations of *Misumena vatia*, a species with similarly extreme SSD. Thus, while extreme SSD may be associated with enhanced mobility of small males during searches for females, it is not precluded by extensive male agonistic encounters.

Keywords: Crab spider, sexual size dimorphism, gravity hypothesis

Members of the thomisine subfamily of crab spiders have played prominent roles in ecological research on spiders. Decades of study by D. H. Morse and his collaborators has made the foraging ecology of *Misumena vatia* (Clerck 1757) among the most thoroughly understood of all predator systems (Morse 2007). The capacity for females of at least six crab spider species to change body color and its impact on foraging has also received substantial attention (e.g., Chittka 2001; Thery & Casas 2002; Heiling et al. 2004, 2005; Herberstein et al. 2009; Brechbühl et al. 2010; Anderson & Dodson 2014). We see a further opportunity for thomisines to play a more significant role in the ongoing investigation of extreme sexual size dimorphism (SSD) in animals. Crab spider females can be more than double the size of males and fully fecund females are many times heavier than adult males (Dondale & Redner 1978; Head 1995; Legrand & Morse 2000). The widely accepted explanation for large females in most invertebrates invokes natural selection for increased fecundity (Darwin 1871; Head 1995; Prenter et al. 1999; Hormiga et al. 2000). By contrast, multiple hypotheses have been proposed to explain small males. A recent phylogenetic analysis of the extremely dimorphic nephilid spiders supports the interpretation that larger body sizes evolved in both females and males, but at a lower trajectory for males (Kuntner & Elgar 2014). Thus, the appropriate question for these and perhaps most spiders might be "What has prevented males from growing as large as females?"

The greatest sexual size disparities among thomisids are represented by *Misumena vatia* and *Misumenoides formosipes* Walckenaer 1837. Small male size and protandry co-occur in both species, but it is uncertain whether one phenomenon determines the other or if selection acts independently on each (Legrand & Morse 2000). Indeed, the mechanisms driving the evolution of protandry across animals in general remain unresolved (Saino et al. 2010). Regardless of the developmental mechanism producing dwarf males, proposals for the selective advantages have been much debated. Ghiselin (1974), Vollrath & Parker (1992) and Vollrath (1998) argued that early maturation at smaller sizes would provide an advantage whenever mating success was determined by a race to find sedentary, unmated females. Elgar (1991) and Elgar & Fahey (1996) championed the notion that dwarf males would have a lowered risk of sexual cannibalism if their size helped them avoid capture or simply made them less attractive as prey. More recently Moya-Laraño et al. (2002) introduced the so-called gravity hypothesis with the basic tenet that males forced to search vertically for females in high habitats will be more successful at smaller body sizes. The latter hypothesis received multiple challenges regarding its applicability across species (e.g., Brandt & Andrade 2007a,b; Prenter et al. 2010) and has undergone subsequent revisions (Moya-Laraño et al. 2009; Corcobado et al. 2010).

An obvious commonality across these hypotheses is that small size provides males with an advantage in mate acquisition due to agility or energy efficiency during travel. Several authors (e.g., Ghiselin 1974; Vollrath & Parker 1992; Legrand & Morse 2000) have highlighted the ecological characteristics expected to promote male dwarfism within spider species according to these hypotheses. They include 1) low population densities (i.e., widely spaced females), 2) protandry, 3) female biased sex ratios, 4) more frequent and longer distance travel by males compared with females

(primarily with vertical challenges vis-à-vis the gravity hypothesis), and 5) limited confrontations between males in cases where large size would otherwise prove advantageous. In this study, we apply new and previously obtained ecological data to examine whether or not the above expectations are met for the dwarf male species *Misumenoides formosipes*. We then compare our findings to those reported for the similar-sized dimorphic *Misumena vatia*.

METHODS

Study species.—*Misumenoides formosipes* is a semelparous speeies widely distributed in North America (Dondale & Redner 1978). Research on this species has focused on its foraging ecology (Schmalhofer & Casey 1999; Schmalhofer 2000; Anderson & Dodson 2014) and mating system; especially faetors determining the outcome of male-male contests during pre-copulatory guarding behavior (Dodson & Beck 1993; Dodson & Schwaab 2001; Hoefler 2002) and navigation cues relevant for mate searches (Stellwag & Dodson 2010; Dodson et al. 2013). Male *M. formosipes* molt into the adult stage over a span that is 1 to 2 weeks ahead of the equivalent span for adult molts in females (G. N. Dodson, pers. obs.).

Spider censuses.—Population censuses were conducted at Ball State University's Cooper Field Area in Delaware County, Indiana between 24 July and 20 August of 2005 and 2006. Intensive searches of the field site by one of us (GND) over many years had revealed that this species has a patchy distribution as late instar juveniles and adults, with spiders typically found where clusters of their preferred pollinator-attracting plants occur. This observation led to the establishment of four census plots of varying sizes (4.6, 6.4, 23.6, and 270.0 m^2) whose dimensions were dictated by the occurrence of discrete clumps of black-eyed Susan (*Rudbeckia hirta*) and Queen Anne's lace (*Daucus carota*). Thus, our estimates reflect high-end population densities rather than average densities across the full field area, most of which has no hunting substrates. Plots were examined every four days unless prevented by inclement weather. When a scheduled census did not oceur, it was conducted as soon as possible and the four-day interval resumed from that day. Censuses involved a thorough search of inflorescences, stems, and leaves within each plot, recording the location and sex of each spider discovered. Densities were calculated as the number of spiders divided by the total area of each plot. Overall estimates of both spider densities and sex ratios were then calculated as the mean of the four plots collectively.

We investigated the population sex ratio again in 2011 by taking advantage of data available from two concurrent projects. Between 24 July and 5 August, males were being collected daily for lab studies from the same area that females were being monitored (without collection) for a field study. Up to six males were collected each day and subsequently released far enough away to avoid being collected again. Meanwhile the locations of all females discovered were marked by hanging a wire clip beneath the inflorescence they occupied and then monitoring their status every 24 h. Females rarely changed location during this time frame and their short moves made it possible to keep track of individuals (see below). While this method of counting the larger, more conspicuous females should have yielded an estimate close to their absolute numbers, we acknowledge that the total number of males was likely underestimated. Even though the counts did not reveal the exact sex ratio, it still allowed us to demonstrate that the population was not female-biased.

Spider movement.—Distances traveled by individual male spiders were quantified using three methods. During August 2004 and 2005 and July 2007 we conducted a total of 16 trials in which four adult males were collected in the field and given unique, dorsal paint marks. Each male was then placed in one of the four cardinal directions at a distance of 2 m from a naturally occurring penultimate female (the stage of females they guard normally). Searches for these marked males were conducted each subsequent day at the same time of day as the original release until none could be located for three consecutive days. The straight line distance between their initial locations (or the last known position if a move had already been recorded) and the location of rediscovery were used to calculate a minimum distance traveled per unit time together with the time that had elapsed. During August 2005 and 2006, >120 marked adult males were released after having been participants in field trials assessing navigational cues (Stellwag & Dodson 2010). Eleven of these males were rediscovered by chance after 24–216 h and their locations relative to initial release points measured. Finally, between 14 July and 8 August 2012 we marked adult (n = 11), penultimate (n = 18), and undetermined (n = 4) males *in situ* and then measured all moves until they could not be relocated for at least three consecutive days.

Locations of juvenile and adult females (n = 84) on the inflorescences of ten plant species were marked with color-coded clips between 18 July and 1 September, 2011. The distance of any subsequent moves were recorded when they were inspected the next day. It was not possible to mark the bodies of the females because they were being studied for color change properties at the same time (Anderson & Dodson 2014). So, while there is a chance that a female could have been misidentified when she moved, the very short average distances moved (see Results) made this unlikely. In 2005 and 2006, we marked and monitored the locations of females discovered in atypical positions (such as on plants with no inflorescences at the time) during routine searches of the field site outside the census plot areas. Tenures for such females are reported separately. All summary statistics are presented as means with standard errors.

RESULTS

Spider censuses.—Plot censuses in both years revealed a slightly female-biased sex ratio in the latter part of July that became male-biased before the end of the month (Fig. 1). During August, males outnumbered females by as much as 2.37:1, after which the numbers of males declined (probably due to male deaths) until well below the number of females (Fig. 1). Changes in the sex ratio were almost certainly due to males from outside the plots arriving at the location of females within the plots.

The male-biased sex ratio found in the 2005/2006 census plots was corroborated by the daily searches of a larger area of the habitat in 2011. The locations of 55 females were marked and monitored over the 13-d span, whereas 72 males were

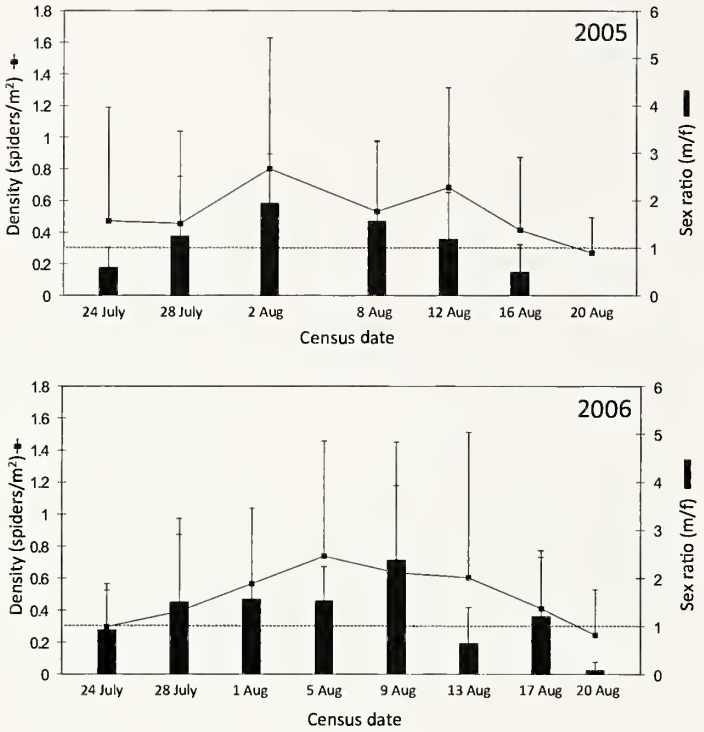

Figure 1.—Mean densities and sex ratios for a population of *Misumenoides formosipes* calculated from censuses of four study plots (see text for descriptions) on the dates noted in 2005 and 2006.

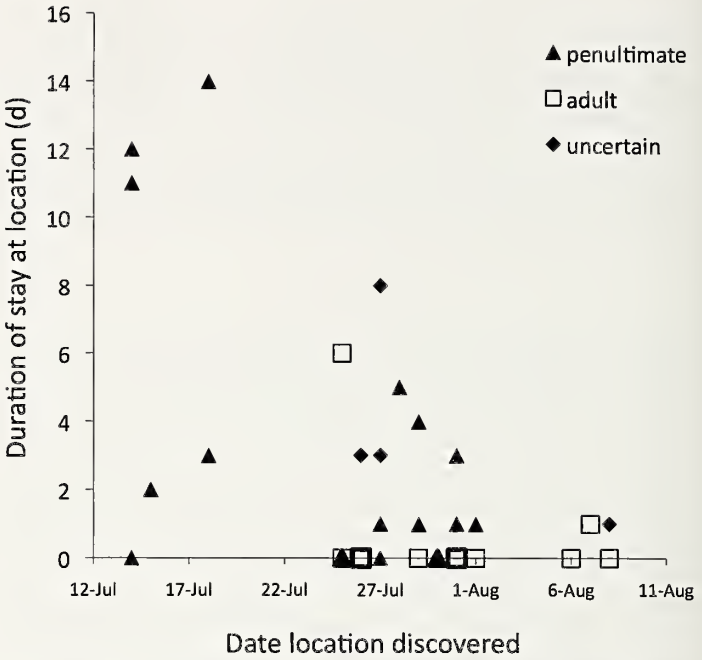

Figure 2.—Number of days *Misumenoides formosipes* males remained on the same plant following the day of discovery for each male in 2012. Symbol type indicates developmental status of each male. Symbols depicted in bold style represent two identical values.

permanently removed from this area over the same time period.

Mean spider densities for the combined plots ranged from 0.26–0.8/m^2 between 22 July and 21 August 2005 (overall mean for all census dates in 2005 = 0.51/m^2) and 0.24–0.73/m^2 over the same time period in 2006 (overall mean for all census dates in 2006 = 0.51/m^2) (Fig. 1).

Spider movement and tenure.—Of the 64 males placed 2 m in the cardinal directions from a penultimate female, all but one had moved from their initial location within 24 h. We rediscovered 45% of these males at least once during daily searches beginning 24 h after release. Ten of these 29 males were rediscovered one to three additional times during further searching. Only two males were re-sighted in the immediate vicinity of the original female 2 m away, but eight males were rediscovered cohabiting with other females in their area. The initial move (i.e., the first time a male was rediscovered regardless of time since trial start) for all 29 males averaged 1.76 ± 0.35 m, which reflects a rate of 0.062 ± 0.012 m/h. Considering only those males that were rediscovered the next day after a trial was started (n = 22), the mean distance moved from the starting point was 1.55 ± 0.35 m for an average rate of 0.064 ± 0.015 m/h. Eight of those same males were relocated during subsequent searches and their new locations reflected greater movement with a mean rate of 0.32 ± 0.25 m/h. The fastest rate of travel measured for any of these trial males was 2.09 m/h, by a male who was relocated at a distance of 7.85 m in 24 h and 16.72 m after 48 h.

Males released after being used in separate navigation research (Stellwag & Dodson 2010) and then rediscovered ca. 24 h later (n = 7) were found an average of 2.86 ± 0.77 m from their release point. The inclusion of four additional males rediscovered 2–4 d after release revealed that the 11 males collectively had moved ca. 3.74 ± 0.97 m/d if their movement had been in a straight line. For comparison with the above "cardinal direction" trial results, this rate of movement would be ca. 0.15 m/h.

Movement by females was limited overall (see below), but we were able to measure moves made by 20 of the 84 immature and adult females monitored in 2011. The average distance from original location to where they were rediscovered the following day for the first move of the 20 females was 0.29 ± 0.049 m. Six of these females made one or two additional moves followed by rediscovery from 1–10 d later. The 29 total moves measured reflected a rate of 0.01 m/h if the spiders' movement was relatively constant and in a straight path. The longest distance from an initial location measured for any female within 24 h was 1.5 m and no other female was discovered more than a meter from her previous location.

Males (n = 33) whose initial location was monitored daily remained on the same plant for 2.42 ± 0.65 d. Forty seven percent of these males had moved from their initial location within 24 h. Of the 29 males whose developmental stage could be confirmed, 18 penultimate instars remained significantly longer (3.22 ± 1.05 d) on a single plant than did 11 adults (0.64 ± 0.54 d) (Mann-Whitney test, U = 50, P = 0.016). Adult male tenure averaged only 0.1 d with the omission of the single outlier who stayed on one plant for 7 days. Tenure on a single plant decreased as the season progressed and this result was driven by a change in the behavior of immature males rather than adults (Fig. 2).

Females monitored for tenure in 2011 (n = 84) remained significantly longer (5.05 ± 0.52 d) at each location than males (2.42 ± 0.65 d, see above) (Mann-Whitney test, U = 1858.5, P = 0.003). Twenty percent of these females had moved from

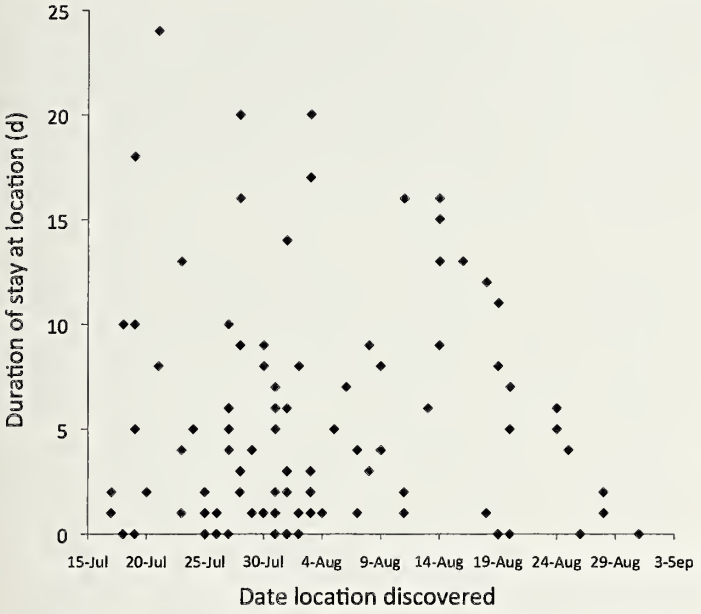

Figure 3.—Number of days *Misumenoides formosipes* females remained on the same plant following the day of discovery in 2011. Data include immature and adult females.

their initial location within 24 h of discovery. Female instar status could not be determined with certainty in many cases and therefore we cannot confirm distinctions between juvenile and adult tenures. The duration of stay for females at a given location decreased across the time period monitored (Fig. 3), most likely a result of adult females moving off inflorescences to preferred locations for depositing egg sacs.

Residencies of females were not limited to positions on inflorescences. Intensive searches from 3–14 August 2006, in areas outside the census plots, revealed 24 females hidden within leaves sealed with silk on plants bearing no open inflorescences at the time. Five plant species were involved with 58% of the sightings on goldenrod (*Solidago altissima*). These females remained at the locations where discovered for an average of 4.12 d (an underestimate since some remained in the same location when monitoring ended).

DISCUSSION

The magnitude of SSD within spiders, particularly in certain families, has been well documented (e.g., Dondale & Redner 1978; Head 1995; Fairbairn 1997; Vollrath 1998; Legrand & Morse 2000). Comparative analyses (Prenter et al. 1999) and phylogenetic studies (Kuntner & Elgar 2014) have supported Darwin's (1871) original thesis that giant females result from natural selection for increased fecundity. In contrast, the selective context for the dwarfism of males in most orb weaver and crab spider species continues to be debated, especially the assumptions and predictions of the gravity hypothesis (Moya-Laraño et al. 2002, 2009; Brandt & Andrade 2007a,b; Prenter et al. 2010; Corcobado et al. 2010). While the significance of climbing to find females deserves investigation, it is only one of many factors suggested to influence male body size in these extreme SSD species.

The mobility enhancement (Ghiselin 1974) and differential mortality (Vollrath & Parker 1992) hypotheses for male dwarfism both imply that traits favoring speed and long distance movement are more important for males than those favoring fighting prowess. Thus, extreme SSD would be more likely in species with low density populations, female biased operational sex ratios (OSR), and scramble competition mating systems with limited male-male agonism. The only one of these expected attributes that characterizes our *M. formosipes* population, however, is the low density, and even that is uncertain (see below). In contrast, we have documented a male biased sex ratio (this study), precopulatory guarding behavior by males (Dodson & Beck 1993), and an advantage of larger size in the frequent and occasionally lethal male-male contests (Dodson & Schwaab 2001; Hoefler 2002). Yet the dwarfed size of males relative to females in this species ranks as one of the most extreme cases across all spiders (Dondale & Redner 1978; Head 1995).

The contrasts between *Misumenoides formosipes* and *Misumena vatia*, the two most dimorphic thomisid species, provide insight into the debate over the causes of male dwarfism. While their foraging ecologies are essentially identical, *M. vatia* differs from *M. formosipes* in having a female biased OSR and scramble competition mating system in which male-male aggressive interactions rarely occur (Holdsworth & Morse 2000; Legrand & Morse 2000; Morse 2007). By contrast, *M. formosipes* males routinely fight over positions near the scarce late-penultimate females (Dodson & Beck 1993; Dodson & Sehwaab 2001). The fact that the two most dimorphic crab spider species exhibit divergent population and mating system characteristics is perhaps our most instructive result. Finding females first or finding females at all during the short adult male lifespan, regardless of the degree of aggressive interference that might follow, seems to be the major driver underlying selection for protandry and small, mobile males.

Movement of males versus females.—A clear prediction of the enhaneed mobility hypothesis for small male size is that males should be moving more frequently and for longer distances than females. Accordingly, we found that the males were more than twice as likely as females to have moved from their initial locations of discovery within 24 h. Those initial moves were six to ten times further for males than females. Other species of non-web building spiders have also exhibited more activity by adult males than females (e.g., Cady 1984; Sullivan & Morse 2004). It should be noted, however, that Vollrath & Parker's (1992) proposal that male dwarfism reduces the risk of mortality was not supported by sexual differences in locomotor behavior *per se* in wolf spiders (Walker & Rypstra 2003).

Sex ratios and densities.—The ease with which these small organisms can disappear from view in their complex habitat forces us to accept that our censuses underestimate the true densities. At the same time, we are confident that our numbers reflect high-end densities across the full field area given that repeated searches always revealed many more spiders at patches of flowers than in between. When *M. formosipes* individuals do show up in flower-less areas, it is more often males than females. Locations chosen for separate navigation trials (Stellwag & Dodson 2010) contained no spiders initially; but as spiders subsequently showed up in the plots, males outnumbered females 48 to 6 over two years. The higher number of males encountered in these "remote" loeations,

coupled with the likelihood of overlooking small, stealthy males versus the more conspicuous females, suggests our male biased sex ratio is also an underestimate.

It is again worth emphasizing the contrast between *M. formosipes* and *M. vatia* populations. Legrand & Morse (2000) reported a range of 2.5–5.1 adult females for every adult male in their populations. Thus, the bias towards females in *M. vatia* was even greater than the bias towards males in our *M. formosipes* population (2.3 males per female at its greatest). The operational sex ratio in our population would be even more biased towards males than the overall sex ratio since the majority of males are adults by the first week of August, whereas most females undergo their adult molts over the next two weeks (G.N. Dodson, pers. obs.).

Comparison of population density values among spider species is hampered by the variation in how they have been measured. In the only other thomisid population density data found, Holdsworth & Morse (2000) completed a month-long census of adult *M. vatia* throughout a 0.5 ha plot via mark/resighting. Their finding of 0.019 spiders/m^2 is an order of magnitude lower than our minimum average densities, but we are confident the difference would be much less if we sampled large plots rather than flower patches. In fact, the largest of our plots (270 m^2) had a lower average density across the two years (0.013 spiders/m^2) than the *M. vatia* counts. Are thomisine crab spider densities low compared with other spiders? Jakob et al. (2011) recorded lower densities than ours for three native linyphiid species in forest habitats, but substantially higher densities for two of the three species in shrubby, coastal habitat. Censuses of two alfalfa field sites revealed densities of ca. three and nine spiders per m^2 for the lycosid *Pardosa agrestis* (Westring 1862) (Kiss & Samu 2000). Both linyphiids and lycosids are much less sexually dimorphic in size than thomisids.

Dwarf males.—Our findings are not the only ones to contradict the prediction that species with dwarf males should exhibit reduced levels of male interactions, especially when large size is an advantage. Foellmer & Fairbairn (2005) also found a male biased OSR and large male fighting advantage in the highly dimorphic orb weaver *Argiope aurantia* Lucas 1833. Kuntner & Elgar (2014) examined studies on sexual selection in nephilid species (the most dimorphic of all spider families) and reported that five out of six documented an advantage for large males in contests on female webs. Given the contrasting patterns for both OSR and the frequencies of male-male interactions in the only two thomisid species measured thus far, more studies of crab spider mating systems are needed for comparison with the orb weaver results.

Male *M. formosipes* are remarkably adept at locating widespread females within a complex habitat. We have documented through field and lab experiments that males are helped in this task at least in part by floral cues (Stellwag & Dodson 2010; Dodson et al. 2013), but this does not account for our observations of males gathering around females on plants far from flower patches. The possibility that female sexual pheromones might aid crab spiders in this quest is contradicted by strong circumstantial evidence in both *M. formosipes* (Dodson & Schwaab 2001) and *M. vatia* (Holdsworth & Morse 2000; Legrand & Morse 2000; Leonard & Morse 2006). Whatever the navigational cues allowing males to find females, the speed at which they are able to climb plant stems and traverse silk lines (bridging) appears to be enhanced by their small size. For both *M. formosipes* and *M. vatia,* the race to find females in these mating systems seems to have a greater influence on male size than does any competitive interactions between rival males should they meet.

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Putative microbial defenses in a social spider: immune variation and antibacterial properties of colony silk

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Abstract. The accumulation of microbes in and around the large, perennial nests of social arthropods can increase the potential for interactions between individuals and harmful pathogens. Accordingly, many social insects utilize multiple organizational lines of individual and collective defenses against microbes. The interaction between microbes and social spiders, however, has been almost entirely unexplored. Here, we use the social spider *Stegodyphus dumicola* Pocock 1898 (Araneae: Eresidae) to (1) probe how innate immunity varies among individuals and (2) determine if two types of silk extracted from their colonies can inhibit the growth of the entomopathogenic bacteria *Bacillus thuringiensis*. Individual spiders' innate immunity against lyophilized cells of *Micrococcus luteus* varied negatively with their boldness, a behavioral metric important for individual foraging and the organization of collective behaviors. Further, silk from both the capture webs and retreats of uncontaminated colonies inhibited the growth of *B. thuringiensis* to a small degree. Thus, web construction might represent a form of collective anti-microbial defense in these social spiders. This preliminary evidence suggests that social spider societies may exhibit antimicrobial defenses on multiple levels of organization, including both individual- and group-level defenses.

Keywords: Antibacterial defense, *Bacillus thuringiensis*, immunity, silk, *Stegodyphus dumicola*

Associations with microorganisms (mutualistic, benign, or harmful) far exceed in frequency any of the other species interactions with which a social animal may be challenged (Ezenwa et al. 2012; McFall-Ngai et al. 2013). Individuals can reduce their likelihood of infection via behavioral (Meyling & Pell 2006), dietary (Singer et al. 2009), or physiological defenses. However, defenses of the arthropod innate immune system can be extremely metabolically costly and social arthropods often exhibit decreased individual-level defenses relative to solitary species (e.g., Freitak et al. 2003; Gwynn et al. 2005; Jacot et al. 2005; Evans et al. 2006). Social insects compensate for these costs, along with their increased risk of disease outbreaks, with a collective "social immunity" via a network of cooperative social interactions (Wilson-Rich et al. 2009; Cremer et al. 2007; Cremer & Sixt 2009). In addition to external sources of pathogens, the physical nests that social arthropods construct can themselves harbor large microbial loads (Hart & Ratnieks 2001; Rosengaus et al. 2003; Chapuisat et al. 2007; but see Wagner et al. 1997). For example, the webs of social spider colonies are often littered with old and fresh prey carcasses (Ward & Enders 1985; Tietjen 1986; Rypstra & Tirey 1991), potentially producing a hotbed for microbial growth (Okafor 1966; Tietjen 1980; Tietjen et al. 1987). How, then, would these seemingly less organized, non-eusocial arthropod societies cope with the increased microbial biota in their nests?

Much of the history documenting the behavioral interactions between spiders and microbes concerns hygienic and sanitary behavior. Hygienic prey carcass-removal behavior has been observed in two African social spiders, *Agelena consociata* Denis 1965 (Furey & Riechert 1989) and *Stegodyplus dumicola* Pocock 1898 (Soydaner 2013). Additionally, the Central American communal mesh-weaver, *Mallos gregalis* (Simon 1909) (Tietjen 1980) and the solitary crab spider *Misumena vatia* (Clerck 1757) (Morse 2008) exhibits sanitary excretory behavior away from their silk, which has been suggested as a means to avoid fouling. These examples illustrate a considerable parallel between the sanitary behavior of social spiders and that of most social insect societies (López-Riquelme & Fanjul-Moles 2013). Conversely, it also appears that *M. gregalis* actually captures new prey that are attracted to the odor produced by yeasts growing on old prey carcasses in the nest (Tietjen et al. 1987), suggesting a positive interaction between some colony-associated microbes and the host spiders. Most important to our understanding of the survivorship of social spider colonies are the descriptions of colony-wide fungal growth in extinct colonies of both old-world and new-world social spiders (Henschel 1998; J.N. Pruitt, pers. comm.). Although it is yet unknown whether fungal epizootics actually cause these colony collapse events, or whether the fungal growth occurs post-mortem, our more detailed understanding of fungal pathogens in non-social spiders suggests these microbes could similarly be important enemies of social spiders (reviewed in Evans 2013). Together, these varied cases demonstrate that more studies are needed to better characterize the nature of social spider/microbe interactions and the mechanisms by which these interactions are carried out.

The general spider immune system has been described in detail (Kuhn-Nentwig & Nentwig 2013). It is similar to the innate immune systems of insects, characterized by a broad defense with limited specificity (Kuhn-Nentwig & Nentwig 2013). Its function is centralized around hemocytes that combat invading cells via phagocytosis, encapsulation, melanization, and the constitutive production of antimicrobial peptides (Fukuzawa et al. 2008; Kuhn-Nentwig & Nentwig 2013). Further, general measures of individual immunocompetence can vary predictably with behavioral traits, as has been described both within and among wolf spiders populations (Ahtiainen et al. 2004, 2005). Recently, González-Tokman et al. (2014) described cuticular antifungal substances in the subsocial crab spider *Diaea ergandros* Evans 1995. Additionally, given that spiders' association with silk encompasses nearly all aspects of their life history (Brunetta & Craig 2010), arachnologists have long speculated that silk may itself contain antimicrobial properties. Recently, Wright &

Goodacre (2012) discovered that silk produced by the common funnel-weaver, *Tegenaria domestica* (Clerck 1757), inhibits the growth of the gram-positive *Bacillus subtilis* in a bacteriostatic fashion. It follows, then, that the webs of social spiders could also exhibit antimicrobial properties, if their silken colonies are indeed at a high risk of accumulating microbes. Here, in a purely exploratory fashion, we probe individual immunity variation and silk-based antibacterial defenses in *S. dumicola*.

METHODS

Animal and bacteria collection.—We collected *S. dumicola* colonies in the southern Kalahari Basin, South Africa, along roadside fences and in *Acacia* bushes. This social spider lives in highly female-biased, inbred social groups of a few dozen up to several hundred individuals (Henschel et al. 1995). Their colonies contain two main functional units: a dense three-dimensional webbed retreat where spiders reside and a cribellate-silk capture web where spiders encounter, capture, and consume prey items (Peters 1992). We collected bacteria from spider cuticles *in situ* by wiping a sterile cotton swab across the entire carapace of one haphazardly chosen adult female spider in each of 20 different colonies in the field. We then plated these samples directly onto lysogeny broth (LB) agar. We did not collect from more than five colonies within 10 km. These plates were incubated at 35°C for 24 h and then stored at 4°C. After bacteria were collected from this subset of spiders, spider colonies and bacterial samples were transported back to the University of Pittsburgh. Individual bacterial colonies were isolated and re-plated several times. After spiders were extracted from their colonies, we measured their body mass (g) using a digital scale immediately before experimentation. Spiders were isolated in 30 ml plastic cups with a piece of chicken wire to facilitate web-building, maintained at ambient temperature and natural light:dark cycles, and fed a diet of one 2-week old domestic cricket weekly. Two spiders from each source colony were used in the immunocompetence assay.

Identification of cuticular bacteria.—Bacterial identification was performed with 300bp 16S ribosomal DNA sequencing and MicroSeq® BLAST Software (SeqWright Genomic Services, Houston, TX 77054). We identified the common gram-positive soil bacterium *Bacillus thuringiensis* on spiders from two colonies approximately 50 km apart. Many common strains of *B. thuringiensis* are generalist entomopathogens (Aronson et al. 1986). We grew *B. thuringiensis* continuously on LB agar plates and maintained them at 4°C. For full BLAST report see Supplemental Material S1, online at http://dx.doi.org/10.1636/M15-12.s1.

Behavioral assays.—To determine if immunocompetence in *S. dumicola* varies with the spiders' behavioral tendencies, we first tested each individual's "boldness" (Sloan Wilson et al. 1994), defined as their latency to resume activity after an aversive stimulus, by simulating the approach of an avian predator (Riechert & Hedrick 1993; Lohrey et al. 2009; Pruitt & Riechert 2012). This behavioral metric is highly repeatable in *S. dumicola* (repeatability ~ 0.63; Keiser et al. 2014a, b) and is positively associated with an individual's propensity to initiate prey capture events (Pruitt & Keiser 2014). We placed spiders (n = 42) in clear plastic arenas (diameter = 12 cm), allowed them a 60 s acclimation period, and administered two rapid puffs of air to the spider's anterior prosoma using an infant nose-cleaning bulb. We then measured the latency for spiders to resume activity (i.e., to move at least one full body length). Trials were terminated after 600 s, and we used the inverse of their latency to move as a metric of their "boldness" (600 minus latency to move, in sec). That is, individuals with long latencies to resume movement had a lower boldness score while individuals that resume movement rapidly have a higher boldness score. Boldness assays were performed between 0900 and 1100 h.

Individual immunocompetence.—We conducted a lytic response assay to estimate the concentration of antimicrobial peptides in the spiders' hemolymph (following the protocol of Ahtiainen et al., 2004, 2005, 2006). We anaesthetized 42 adult female *S. dumicola* with CO_2 and extracted a 0.5 µl sample of hemolymph from a puncture directly posterior to the epigastric furrow using a sterilized Hamilton syringe. Hemolymph samples (n = 42) were mixed with 20 µl of 0.01M phosphate buffered saline (PBS), vortexed at 1500 rpm for 3 s, and frozen at -80°C. Thawed samples were vortexed at 1500 rpm for 3 s and pipetted into a 96-well flat-bottom microplate. Then, all samples were mixed with 80 µl of a 0.20 mg/ml PBS solution of lyophilized *Micrococcus luteus* cells (Sigma Chemical Co.; St. Louis, MO) and vortexed at 1500 rpm for 3 s. We then measured the samples' optical density at 492 nm immediately after mixing and again after 10 minutes using a BioTek Microplate reader (BioTek US, Winooski, VT). The strength of the immune response is determined by the magnitude by which the optieal density of the solution decreases over this time. Frozen and thawed hemolymph was used as a control (n = 10). Due to an increase in optical density via sedimentation of the hemolymph suspension, the mean amount by which control samples increased in optical density (change in optical density = 0.0043) was subtracted from the observed values of experimental samples.

Antibacterial properties of silk.—We placed 10 adult female spiders originating from the same source colony into a clean 500 ml plastic cup with a piece of sterilized chicken wire to facilitate web construction (n = 12 experimental colonies from 12 different source colonies). These spiders were not fed in these cups, and they remained sealed for one week to allow spiders to produce new silk in an environment uncontaminated by prey or prey remains. We tested this silk for antibacterial properties against a strain of *B. thuringiensis* collected from the cuticle of an adult female *S. dumicola in situ* (described above). We created a lawn of bacteria on a petri dish containing LB agar by applying 20 µl of a liquid bacterial culture of *B. thuringiensis* grown in LB broth at 35°C for 24 hours and spread the solution evenly using a sterile inoculating loop (Thermo Fisher Scientific Inc., Waltham, MA). This was performed immediately prior to applying the spider silk.

We used sterilized forceps to wrap a thin layer of silk around a sterile filter paper disk (diameter = 6 mm), dipped it in ethyl acetate, an organic solvent commonly used for extractions of antibiotics (Dutia 2004), and placed it directly onto the surface of the agar, leaving the silk strands intact. Preliminary experiments suggest that ethyl acetate itself does not have antibacterial activity against *B. thuringiensis* (unpubl.

data). However, to test whether any antibacterial activity observed was due to the structural properties of the silk, or one of its chemical constituents, we also mixed separate silk samples with 0.5 ml of ethyl acetate and vortexed them for 15 s. We then dipped filter paper disks in this solution and applied the disks to the agar surface as before. Control disks were dipped only in ethyl acetate. We performed this assay with both silk types that are used in the construction of *S. dumicola* colonies: (1) non-sticky retreat silk and (2) capture web cribellate silk (n = 15 disks per treatment allocated across 15 petri dishes). Each petri dish contained 6 different disks: (1) vortexed capture silk, (2) vortexed retreat silk, (3) intact capture silk, (4) intact retreat silk, (5) ethyl acetate control, and (6) an untreated filter paper disk control. The petri dishes were incubated at 35°C for 24 h, after which we then measured the annular radius of the zones of inhibition around the disks.

Statistical analyses.—We used non-parametric Spearman's rank correlation to test the relationships between individual boldness, body mass, and immunocompetence (i.e., hemolymph lytic activity). To test the effects of spider silk on bacterial growth, we used a general linear mixed model with treatment as an independent variable and the radius of the zone of inhibition as the response variable. Source colony ID and treatment nested in agar plate ID were included as random effects. All statistical analyses were performed in JMP version 10 (SAS Institute Inc., Cary, NC, USA).

RESULTS

Individual immunocompetence.—Hemolymph collected from spiders with a greater measurement of boldness exhibited a weaker immune response when compromised with the bacteria *M. luteus* (mean change in optical density = –0.01, SE = 0.005; Spearman's $\rho = 0.33$, df = 40, $P = 0.04$; Fig. 1). Although boldness was negatively correlated with body mass (Spearman's $\rho = -0.44$, df = 40, $P = 0.009$), our measure of innate immunity only showed a non-significant positive trend with body mass (Spearman's $\rho = -0.30$, df = 40, $P = 0.08$).

Antibacterial properties of silk.—Filter paper disks wrapped with intact silk inhibited the growth of the bacteria *B. thuringiensis* while disks dipped in a silk-ethyl acetate solution were not significantly different from the control treatment ($F_{4, 89} = 7.23$, $P < 0.0001$; Fig. 2). Intact spider silk produced zones of inhibition, though relatively small on average, over four times larger than any other treatment type. There was no difference in the antimicrobial activity of silk originating from two different parts of the colony, the capture web vs. the retreat (Fig. 2).

DISCUSSION

Interactions between microbes and hosts by and large represent the most common ecological interaction in which any animal or plant participates. Large, stable animal societies must therefore exhibit antimicrobial defenses across multiple levels of organization (e.g., individual and collective defenses). Here, we demonstrated that individuals' innate immune responses to lyophilized bacterial cells varied negatively with their boldness in the social spider *S. dumicola*. We also demonstrated that two functionally different silks used to construct *S. dumicola* colonies can weakly inhibit the growth of the gram-positive entomopathogen *B. thuringiensis*.

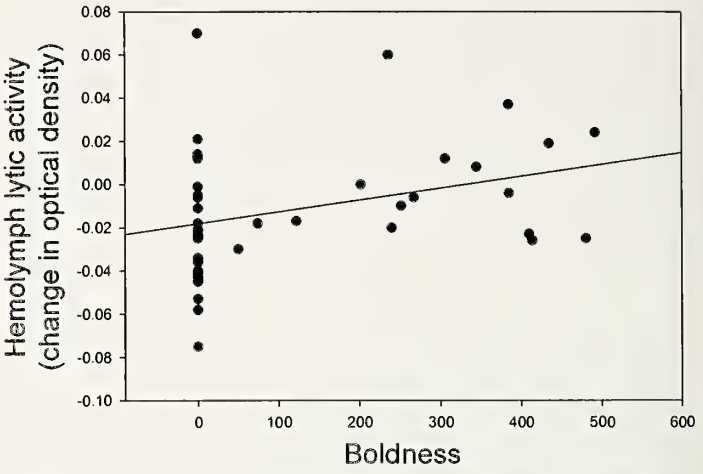

Figure 1.—Individuals with greater boldness values (i.e., those that resumed activity faster during our boldness assay) were associated with decreased lytic activity relative to shy spiders, suggesting a weaker immune response (Spearman's $\rho = 0.33$, df = 40, $P = 0.04$). Lytic activity values below zero indicate a decrease in optical density over the sampling interval, suggesting a stronger lytic activity.

We identified a negative relationship between individual boldness and innate immune defense. Many studies have demonstrated that individuals with higher boldness or more pronounced behavioral traits (e.g., sexual advertisement, anti-predator behavior) have a weaker investment in immune defenses (Rigby & Jokela 2000; McKean & Nunney 2001; Roberts et al. 2004; Ahtiainen et al. 2005; Kortet et al. 2007; Niemelä et al. 2012). This trade-off between individual immunity and other traits like anti-predator behavior should be expected based on traditional life history theory (Stearns 1992; Norris & Evans 2000; Zuk & Stoehr 2002). However, the magnitude by which individual immunocompetence and other behavioral traits are negatively related should be contingent

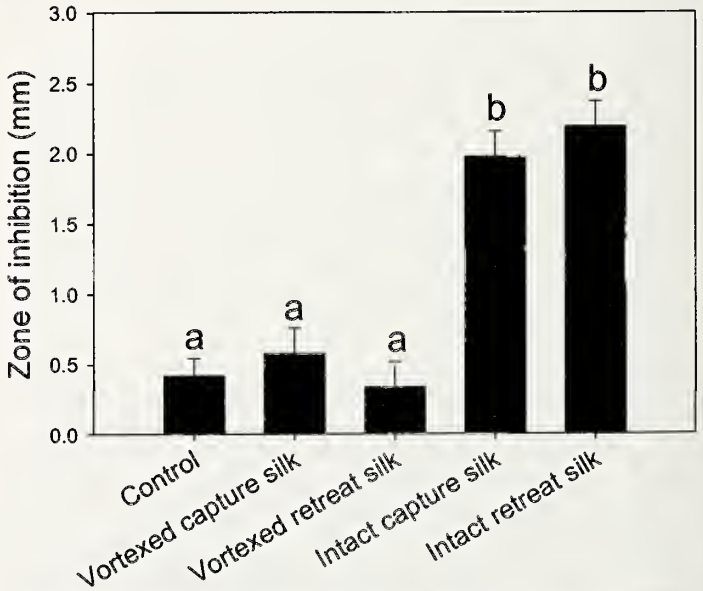

Figure 2.—Intact spider silk from both the capture web and retreat significantly inhibited the growth of *B. thuringiensis* ($F_{4,89} = 7.23$, $P < 0.0001$). Bars significantly different from one another are denoted with different letters (Tukey's HSD post-hoc test).

on whether or not the behavior of interest is indeed metabolically costly (Norris & Evans 2000).

Alternatively, *positive* relationships between measurements of immunity and behavioral traits like social dominance (Zuk & Johnsen 2000; Ahtiainen et al. 2006) and resource holding potential (Koskimäki et al. 2004) have also been documented. The mechanistic underpinnings of the boldness/immunity relationship in this system are entirely unknown. Although we found no relationship between body mass and immunity, the relationship between immunocompetence and nutritional gain/feeding rate should be explored further (Chandra 1983; Saino et al. 1997). Bold individuals initiate more foraging events (Pruitt & Keiser 2014) and are the first to begin eonsuming the subdued prey item, thus gaining the greatest nutritional benefit from the foraging bout (Amir et al. 2000). Perhaps, though, this investment in extra-oral digestion is metabolically costly and is related to other systems of innate immunity (Haeberli et al. 2000). Further, we observed broad variation in immunity among individuals that reeeived a boldness value of 0, potentially because the 600 s cutoff for our boldness assay truncates the data set and does not account for variation among individuals beyond that point. Future studies on the relationship between behavioral traits and immunity should allow for a larger window of measurements.

It should be particularly profitable to investigate both social and solitary species of *Stegodyphus* in unison to test the hypothesis that individual investment in immune defenses increases with sociality or perhaps that among-individual variance in immunity is greater in social species (Wilson et al. 2003). *Stegodyphus* spp. represent a promising case to test within-colony or within-family pathogen transmission, as adult females are consumed by their offspring at the end of their lives (Seibt & Wickler 1987; Schneider 2002; Salomon et al. 2005; Ruch et al. 2012). Given that pathogen transmission is commonly regarded as a selective force against cannibalism, especially among kin, the role of this pivotal life-history event in colony health is particularly intriguing (Pfennig 1997; Pfennig et al. 1998).

Just like the way many soeial insects collect and prophylactically treat their colonies with antimicrobial substances (Christe et al. 2003; Chapuisat et al. 2007), social spiders may similarly be able to reduce microbial growth via the antibacterial properties of their silk. Our results indicate that intact silk limits bacterial growth while ethyl acetate impregnated with silk had no antibacterial properties. Wright & Goodacre (2012) demonstrated that silk treated with Proteinase K had a reduced antimicrobial ability, suggesting that one or more protein elements are involved as active agents. Here, the lack of antibacterial activity in the vortexed silk may have been a result of a dilution in the concentration of products exhibiting the antibacterial activity. Sanggaard et al. (2014) recently discovered ~132 proteins in the silk of the social spider *S. mimosarum* Pavesi 1883, which is a key step to identifying the causative agents of antimicrobial activity.

The zones of inhibition produced around the silk-treated disks were relatively minor compared to the inhibition of other *Bacillus* spp. by commercial antibiotic extractions (Coonrod et al. 1971). We are unsure if this is because of the actual inhibitory nature of spider silk or a low concentration of antibacterial properties due to our extraction methods. Regardless, this research provides an important step towards understanding collective antimicrobial defenses in social spiders, a group wholly ignored in the ecoimmunology literature. Future studies should employ dilution techniques to determine the minimum inhibitory concentration (i.e., mass of silk) necessary to inhibit bacterial growth, and attempt to identify the causative antimicrobial agents via proteomic methodologies.

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Effects of hedgerows and riparian margins on aerial web-building spiders in cereal fields

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Abstract. Spiders (Araneae) are dominant predators in agro-ecosystems. Terrestrial seminatural habitats, such as hedgerows and grassy field margins, can enhance the abundance and diversity of spiders in adjoining fields, whereas the potential of riparian margins has rarely been studied. We compared the effects of hedgerows and riparian margins on aerial web-building spiders in adjacent cereal fields. While species richness and overall abundance did not significantly respond to distance from or type of field margin, each of the four dominant species responded differently. The abundance of *Tetragnatha* cf. *montana* Simon 1874 increased towards both hedgerows and riparian margins. *Tetragnatha extensa* (Linnaeus 1758) differentiated between field margin types and abundances increased only towards riparian margins. By contrast, *Phylloneta impressa* (L. Koch 1881) abundances decreased from field centers towards the field margins irrespective of the type. Type of field margin and distance showed an interactive effect on *Mangora acalypha* (Walckenaer 1802) abundances, which decreased from field centers towards hedgerows but changed only little towards riparian margins. Increasing spider densities towards field margins can be explained by the preference of spiders for adjoining seminatural habitats (overwintering, food availability, microclimate, vegetation structure), whereas increases towards field centers might be caused by interspecific competition and enhanced predation pressure near seminatural habitats and high prey numbers in crop fields. Overall, our study demonstrates that aerial web-building spider species respond differently to hedgerows and riparian margins.

Keywords: Agro-ecosystems, Araneae, edge effects, seminatural habitat

Spiders (Araneidae) are among the most abundant and species-rich invertebrate predators in agricultural landscapes. They are important predators of crop pests, and high spider abundance and diversity are important for successful biological control (Marc et al. 1999; Nyffeler & Sunderland 2003). Agro-ecosystems are usually dominated by few spider species (Schmidt & Tscharntke 2005; Prieto-Benitez & Méndez 2011) and, in Europe, less than ten agrobiont species constitute 60–90% of the individuals of spider communities in fields with only little variation among crops and regions (Samu & Szinetár 2002).

Most agricultural landscapes are a mosaic of fields, seminatural habitats (e.g., field margins, hedgerows) and roads (Marshall & Moonen 2002). Spiders use seminatural habitats as refuges during disturbances in the field (ploughing, harvesting, pesticide application), for overwintering and as source habitat for recolonization (Pfiffner & Luka 2000; Prieto-Benítez & Méndez 2011). Additionally, seminatural habitats provide alternative food sources and complex vegetation structures for web attachment (Dix et al. 1995). Thus, seminatural habitats subsidize within-field spider populations and can enhance the predation pressure on crop pests (Clough et al. 2005; Öberg et al. 2008). These positive effects often decline with increasing distance from the field margin (Denys & Tscharntke 2002), usually within a few or tens of meters (Dennis & Fry 1992; Bedford & Usher 1994; Sunderland & Samu 2000). However, opposite patterns with higher spider abundances within crop fields have also been reported (Birkhofer et al. 2014).

Most studies analyzing the effects of seminatural habitats on spiders in fields focussed on terrestrial habitats such as forest edges (Bedford & Usher 1994; Kajak 2007; Oleszczazuk et al. 2010) or grassy field boundaries (Dennis & Fry 1992; Baines et al. 1998; Huusela-Veistola 1998; Denys & Tscharntke 2002, Birkhofer et al. 2014). In contrast, studies analyzing the effects of riparian margins on spiders in crop fields are scarce. In addition to their function as refuge habitat, riparian margins can provide supplemental food to spiders in adjoining crop fields. Fluxes of aquatic insects emerging from streams can be as high as 10,000–20,000 insects m^{-2} $year^{-1}$ (mainly adult Diptera, Ephemeroptera, Plecoptera, Trichoptera and Odonata) and can provide an important energy subsidy to adjacent terrestrial habitats (Baxter et al. 2005). Emergence may exceed terrestrial production per unit area in the surrounding landscape, especially in May and June, when emergence is usually highest in temperate zones. This additional prey-availability can lead to high densities of consumers in aquatic-terrestrial ecotones independent of the habitat type (Kato et al. 2003; Ballinger & Lake 2006), though this can be affected by land use (Krell et al. 2015; Stenroth et al. 2015). Aquatic prey can be an important component of spider diets, up to 99% in Tetragnathidae and 64% in Linyphiidae and, hence, might influence the biomass, abundance and species composition of spiders (Iwata 2007). Thus, the abundance of web-building spiders can be enhanced by emergence and be related to the proximity to the body of water (Henschel 2004; Iwata 2007; Marczak & Richardson 2007; Burdon & Harding 2008). In turn, the emergence can indirectly lead to a higher predation on terrestrial herbivores (Henschel et al. 2001; Henschel 2004). However, most of these findings are based on studies of forest–stream boundaries.

We examined the influence of streams on aerial web-building spiders in adjacent crop fields and compared the effects of hedgerows and riparian margins. We tested the following hypotheses: (i) the type of field margin (riparian margin, hedgerow) influences the composition, abundance and species richness of spiders in adjoining fields, with (ii) riparian margins exhibiting a stronger influence than hedgerows, and (iii) decreasing influence with increasing distance to the field margins.

Table 1.—ANODEV table of the effect of field margin type and distance from the field margin on spider species richness, overall abundance, and abundance of the four dominant species (quasi-Poisson GLMM). Significant *P*-values are marked with asterisks ('*' $P < 0.05$, '**' $P < 0.01$), '***' $P < 0.001$).

	Distance (log transformed)			Field margin type			Distance x margin		
	df	t	*P*	df	t	*P*	df	t	*P*
Species richness	39	−1.68	0.10	3	−0.93	0.42	–	–	–
Overall abundance	38	2.01	0.051	3	3.10	0.053	38	−2.86	0.007**
Mangora acalypha	38	2.55	0.015*	3	3.14	0.052	38	−2.31	0.027*
Phylloneta impressa	39	4.68	<0.001***	3	−0.91	0.43	–	–	–
Tetragnatha extensa	38	1.80	0.080	3	3.35	0.044*	38	−2.66	0.012*
Tetragnatha cf. *montana*	38	−3.71	0.001**	3	0.56	0.62	38	−3.27	0.002**

METHODS

We investigated four conventionally managed winter cereal fields in an intensely used agricultural landscape near the city of Landau, Germany (49°12N, 8°7E). Prior to sampling, only herbicides, which are typically not directly toxic to arthropods (Bell et al. 2002; Pékar 2002), were applied to the fields. The fields had a size of at least 2 ha and were bordered at one side by a hedgerow and on the opposite side by a riparian margin. At two sampling sites, the two different field margins belonged to different adjacent fields with the same crop type. Three hedgerows and three riparian buffer strips were adjacent to wheat fields (*Triticum aestivum*), while one hedgerow and one riparian buffer strip were adjacent to rye fields (*Secale cereale*). Hedgerows had a width of about four meters and were dominated by shrubs such as *Rubus* sp., *Rosa canina*, *Sambucus nigra*, *Prunus spinosa*, and *Cornus sanguinea*. Riparian margins were three to five meters wide and had a dense and tall herb and grass layer. On the other side of the stream was a three meter broad hedgerow with trees.

Twelve transects were made in each field, i.e., six transects per field margin at distances of 1, 3, 5, 9, 17 and 25 meters into the field (N_{total} = 48 transects with an area of ca. 3,840 m^2). To account for possible confounding effects, structural parameters of the fields and the field margin were recorded (Appendix 2). Aerial web-building spiders were sampled between 13 and 21 May 2011, when the recolonization of spiders from the field margins should have occurred and the emergence of aquatic insects is expected to be high (Kato et al. 2003; Öberg et al. 2008). Spiders were sampled by sweep netting under dry and warm weather conditions, which is an effective method to catch web-building spiders in the vegetation layer (Amalin et al. 2001). A sweep net with a diameter of 30 cm was moved 200 times per transect corresponding to a length of approximately 40 m and a width of 2 m per transect (area = 80 m^2 per transect).

Web-building spiders were identified alive in the field or, if necessary, in the laboratory. Identification and nomenclature followed Roberts (1996) and World Spider Catalog (2015). A few spiders were only identified to genus level and, within the genus *Tetragnatha* Latreille 1804, we only distinguished between *Tetragnatha extensa* (Linnaeus 1758) and *Tetragnatha* cf. *montana* Simon 1874 (comprising all individuals with uniformly dark sternum). Spider density per square meter was calculated by dividing the number of individuals by the area sampled. Note that these results are lower-bound abundance estimates, because of limited sampling efficiency.

The explanatory power of environmental variables (Appendix 2) for community composition was assessed using permutational analysis of variance (PERMANOVA) (Anderson 2001) with Bray Curtis dissimilarity as distance measure (function 'adonis' in R package "vegan", Oksanen et al. 2010). We used strata to account for our nested design (strata = field). The number of species and individuals were related to the field margin type and the distance to the field margin with generalized linear mixed models (GLMM) using the function glmmPQL (packages "MASS", Venables & Ripley 2002, and "nlme", Pinheiro et al. 2009). The function glmmPQL fits GLMM via penalized Quasi-Likelihood. We used a Poisson GLMM for count data and corrected the standard errors based on a quasi-Poisson model because overdispersion was detected. We used field margin type and the distance to the field margin as fixed effects and transects nested in field as a random effect. Distances from the field margin were log(x+1)-transformed to account for the expected exponential change of spider abundance from the margin towards the field centers, owing to the likely exponential decrease of the aquatic prey within a short distance to the field margin (Sunderland & Samu 2000). Interaction terms between distance and type of field margin were only retained in the models if significant. Model performance was checked graphically using diagnostic plots and potential outliers were identified using Cook's distance (Zuur et al. 2009). Statistical analyses were done in R 3.1.2 (R Development Core Team, 2014).

RESULTS

Overall, 767 individuals of aerial web-building spiders from the families Araneidae, Linyphiidae, Tetragnathidae and Theridiidae were caught (spider density = 0.2 ind/m^2) (Appendix 1). Eighteen juveniles of Araneidae and Linyphiidae were excluded from further analysis because they were too small for identification. The remaining individuals comprised 14 genera and 16 species. Most abundant were *Mangora acalypha* (Walckenaer 1802) (49%), *Tetragnatha extensa* (19%), *Phylloneta impressa* (L. Koch 1881) (16%), and *Tetragnatha* cf. *montana* (6%). All other species accounted for less than 1% of all individuals. The composition of spider assemblages was significantly affected by the distance from field margins, but not by any of the remaining habitat parameters (Appendix 2). Species richness and overall abundance of web-building spiders was not significantly related to the field margin type (hedgerow or riparian margin) or the distance to the margin (Table 1). By contrast, the field margin type and the distance to the margin significantly

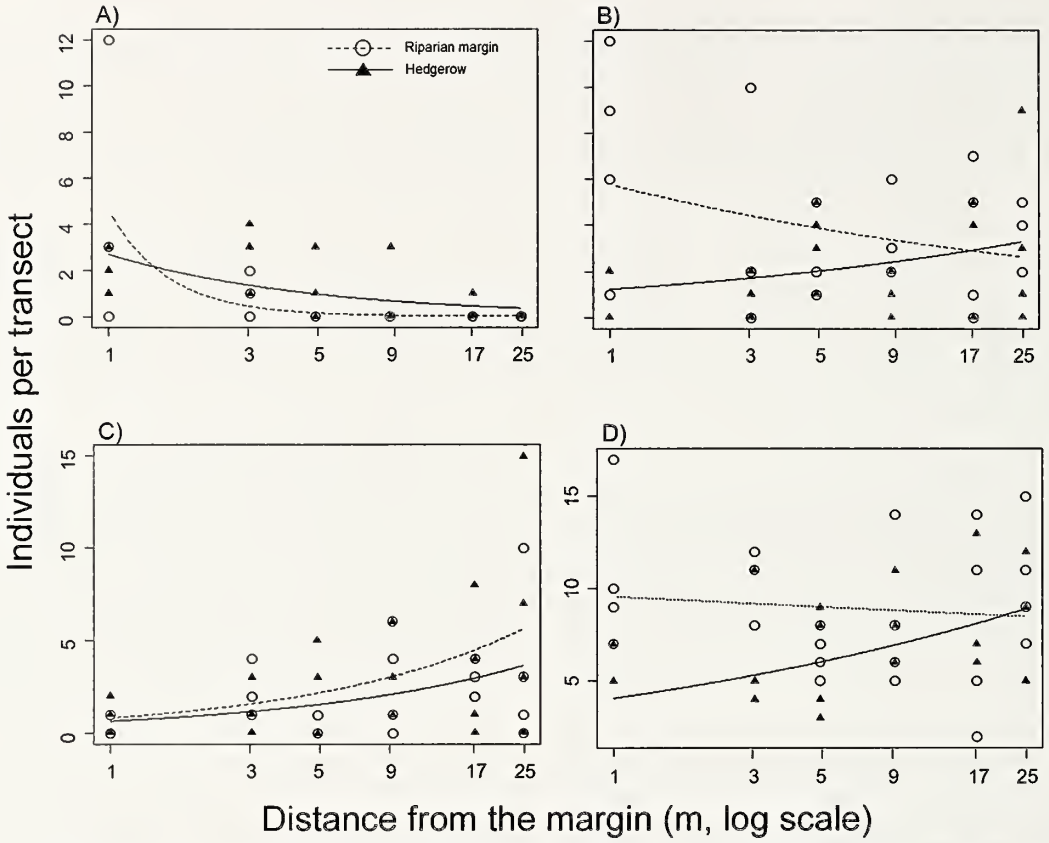

Figure 1.—Effects of field margin type and distance from field margin on the abundance of A) *Tetragnatha* cf. *montana* (hedgerow: $P < 0.001$, riparian margin: $P = 0.007$); B) *Tetragnatha extensa* (hedgerow: $P = 0.085$, riparian margin: $P = 0.125$); C) *Phylloneta impressa* (hedgerow: $P = 0.011$, riparian margin: $P = 0.026$); D) *Mangora acalypha* (hedgerow: $P = 0.013$, riparian margin: $P = 0.630$).

affected the four most abundant species (Table 1). Abundances of *T.* cf. *montana* increased from the field centers towards both margin types (Fig. 1A). Abundances of *T. extensa* responded significantly to the interaction of margin type and distance. Abundances increased towards riparian margins from the field centers, but decreased towards hedgerows (Fig. 1B). The abundance of *P. impressa* decreased towards both field margin types (Fig. 1C). Type of field margin and distance to the margin showed an interactive effect on *M. acalypha* abundances, which decreased from field centers towards hedgerows but changed little towards riparian margins (Fig. 1D).

DISCUSSION

Our results showed that the type of field margin and the distance to the margin affected spider species abundances differently, leading to a change in species composition rather than to a change in overall abundance or species richness. Such patterns are known for ground-dwelling spiders (Clough et al. 2005; Schmidt-Entling & Döbeli 2009) and for other macro-invertebrates (Holland et al. 1999; Anjum-Zubair et al. 2010; Hof & Wright 2010), but, to our knowledge, not for spiders that build their webs high in the vegetation. In the following, we describe the patterns of the four dominant species and discuss potential mechanisms.

Abundances of *T.* cf. *montana* increased from the field centers towards both margin types, whereas *T. extensa* abundances increased only towards riparian margins. The increase of both *Tetragnatha* species towards field margins can be explained by the general preference of spiders for field margins, which offer suitable overwintering sites, alternative food, microclimate, and vegetation structure. First, most spiders overwinter outside arable fields, and recolonize from the margin (Dix et al. 1995; Pfiffner & Luka 2000; Öberg et al. 2008). Spiders heavier than 15 mg cannot disperse via ballooning, and cursorial movement is less effective for moving far into the fields (Samu et al. 1999; Bell et al. 2001; Entling et al. 2011). As a result, the interior of arable fields is likely to be colonized mostly by small spiders, for most families by younger instars, which are able to balloon (Samu & Szinetár 2002). Individuals that are too large for ballooning or species that never balloon should be restricted to areas near the field margin. All abundant spider species in this study are able to balloon (Bell et al. 2005). However, *Tetragnatha* sp. balloon mostly as immatures and may be too heavy for aerial dispersal during spring (Nyffeler & Benz 1989; Blandenier 2009), which may explain the increased *Tetragnatha* densities towards field margins. Second, food availability can be higher in field margins than in field centers (Huusela-Veistola 1998). Hence, the concentration of spiders near the field margin can be caused by their preference for web sites with high prey resources (Harwood et al. 2003). Moreover, *Tetragnatha* sp. are positively related to aquatic insect flux and react strongly to the availability of aquatic prey (Kato et al. 2003; Baxter et al. 2005; Iwata 2007; Marczak & Richardson 2007). This can

explain the differentiation of *T. extensa* between hedgerows and riparian margins in this study. Third, fields and margins differ in microclimate and moisture, which are important factors for the distribution and web site selection of spiders (Samu et al. 1999; Bell et al. 2001). The sensitivity of *Tetragnatha* sp. to desiccation might be a further explanation for their preference for moist conditions near streams (Power et al. 2004). Finally, web-building spiders often prefer microhabitats with complex vegetation structure (Bell et al. 2001) and vegetation in cereal fields is generally more homogeneous than in field margins (Cole et al. 2005).

Both *M. acalypha* and *P. impressa* showed increased abundances towards the field center. For *M. acalypha*, the increase towards the field center was especially high at hedgerows while *P. impressa* preferred field centers regardless of the field margin type. In contrast to *Tetragnatha* sp., these species are able to balloon in spring, which enables an effective dispersal far into the fields (Blandenier 2009), and are less responsive to aquatic prey (Iwata 2007). Among farmland spiders, *P. impressa* is one of the species with the strongest preference for fields over perennial habitats during the vegetation period (Schmidt & Tscharntke 2005), which may be explained by the availability of high prey numbers during certain parts of the season (Pekár 2000; Jurczyk et al 2012). However, *P. impressa* does not appear to overwinter in arable fields (Pfiffner & Luka 2000), suggesting that it actively moves into cereal fields. A reason for its preference for field interiors might be avoidance of competition and predation (Sunderland & Samu 2000). Intraguild interference in structurally simple agro-ecosystems is often high, and at low prey density, many spiders feed on other spiders (Nyffeler 1999). *Phylloneta impressa* is a powerful colonizer that can easily reach central parts of crop fields in contrast to many of their intraguild competitors (Blandenier 2009). In the presence of chemical cues of ants, *P. impressa* increase their propensity for silk-based dispersal (Mestre et al. 2014). Thus *P. impressa* may prefer field centers to avoid interference with species that are limited to the vicinity of the margins. Furthermore, a higher predation pressure along seminatural habitats can be assumed. For example *P. impressa* and *M. acalypha* are the main prey of *Trypoxylon figulus* (Linnaeus 1758), a wasp that is particularly abundant along woody habitats such as hedgerows (Coudrain et al. 2013). Thus, field centers may represent areas of both low competition and low predation pressure for both spider species.

To conclude, aerial web-building spiders showed species-specific responses to the distance and type of field margin. The lack of an overall positive influence of riparian margins on spiders in arable fields contrasts with findings from more natural systems. Future studies should explore whether environmental stress on streams (e.g., in the form of agricultural inputs) can explain the lack of a more positive influence on terrestrial predators. The potential role of predators and competitors in reducing spiders near field margins could be resolved with field experiments.

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Appendix 1.—Abundance of the web-building spiders per transect at 1, 3, 5, 9, 17, and 25 m distance from the field margin, shown separately for riparian margins (r) and hedgerows (h).

		Distance from the field margin [m]													
		1		3		5		9		17		25			Individuals
Family	Species	r	h	r	h	r	h	r	h	r	h	r	h	Total	per 100 m^2
Araneidae	*Araniella cucurbitina* (Clerck 1757)	0	0	1	0	0	1	0	0	0	0	1	0	3	0.08
	Argiope bruennichi (Scopoli 1772)	0	0	0	0	0	0	0	0	0	1	0	0	1	0.03
	Hypsosinga sanguinea (C. L. Koch 1844)	0	0	0	0	0	1	0	0	0	0	0	0	1	0.03
	Mangora acalypha (Walckenaer 1802)	43	13	39	24	26	24	33	33	32	33	42	31	373	9.71
	Unidentified juvenile	2	2	0	4	1	1	1	0	0	4	0	1	16	0.42
Linyphiidae	*Erigoninae* sp.	4	4	0	1	1	0	0	0	0	1	0	1	12	0.31
	Tenuiphantes tenuis (Blackwall 1852)	0	0	0	0	2	1	0	0	1	1	1	0	6	0.16
	Unidentified juvenile	0	0	0	1	0	1	0	0	0	0	0	0	2	0.05
Tetragnathidae	*Metellina mengei* (Blackwall 1869)	3	3	0	0	0	0	0	0	0	0	0	0	6	0.16
	Tetragnatha extensa (Linnaeus 1758)	18	6	14	3	10	13	14	5	13	14	13	13	146	3.8
	Tetragnatha cf. *montana* Simon 1874	18	7	3	11	0	4	0	3	0	1	0	0	47	1.22
Theridiidae	*Achaearanea sp.* (Strand 1929)	0	0	0	0	0	0	1	0	0	0	0	0	1	0.03
	Enoplognatha ovata (Clerck 1757)	1	0	0	0	0	1	0	0	0	0	0	0	2	0.05
	Neottiura bimaculata (Linnaeus 1767)	12	1	3	1	2	2	1	1	0	1	2	0	29	0.76
	Phylloneta impressa (L. Koch 1881)	1	3	9	4	2	13	11	13	11	13	14	25	119	3.1
	Steatoda sp. Sundevall 1833	0	0	0	0	0	0	0	0	1	0	0	0	1	0.03
	Theridion pinastri L. Koch 1872	0	0	0	0	0	0	0	0	0	0	0	1	1	0.03
	Theridion sp. (Walckenaer, 1805)	0	0	0	0	0	1	0	0	0	0	0	0	1	0.03
Total		112	39	69	49	44	63	61	55	58	69	73	75	767	19.97

Appendix 2.—Effect of field margin type, distance from the field margin and vegetation parameters on spider species composition. The explanatory power of environmental variables was assessed using permutational analysis of variance with pseudo-F ratios and partial R^2 values. The Bray Curtis dissimilarity was used as distance measure and strata to account for the nested design (strata = field). Within the fields, vegetation cover (%) was estimated at four 1-m^2 plots every 10 m per transect. In each plot the vegetation height was measured five times with a round disk (diameter: 19 cm, weight: 50 g), which was dropped from a standardised height of 1 m. The height of the grass and the shrub layer of the field margins were quantified eight times every 5 m. The height of the grass layer was measured using a round disk as in cereal fields. The height of the shrub layer was calculated with a declinometer. Significant *P*-values are marked with asterisks ('***' $P < 0.001$).

	Interval (min – max)	F	R^2	*P*
Field margin type	riparian, hedgerow	1.0	0.02	0.43
Distance from field margin (log transformed)	1– 25 m	7.3	0.13	0.001***
Vegetation cover in field	20 – 55%	1.2	0.02	0.45
Vegetation cover in field margin	59 – 100%	2.0	0.04	0.072
Vegetation height in field (mean)	0.31– 0.59 m	1.6	0.03	0.28
Herbal height in field margin	0 – 0.65 m	2.6	0.05	0.19
Shrub height (mean)	2.7 – 21 m	0.3	0.01	0.94

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Neochelanops michaelseni (Pseudoscorpiones: Chernetidae) as a potential bioindicator in managed and unmanaged *Nothofagus* forests of Tierra del Fuego

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Abstract. Bioindicators could act as early warning indicators of environmental changes, ecosystem stress or taxonomic diversity. Pseudoscorpions have rarely been used as bioindicators, due to lack of information about their ecology, habitat selection, niche preferences and requirements, especially in southern *Nothofagus* forests. We studied the distribution and abundance of a pseudoscorpion species, *Neochelanops michaelseni* (Simon 1902), in different vegetation types (*Nothofagus antarctica* and *N. pumilio* forests, grasslands and peatlands) and examined how this species responded to different forest uses (harvesting and silvopastoral management), to explore its utility as a bioindicator. The study was conducted on long-term plots located at two ranches in Tierra del Fuego, using pit-fall traps during one summer. *Neochelanops michaelseni* abundance was higher in *Nothofagus* forests than in open ecosystems, which could be attributed to their affinity for litter and coarse woody debris. In *N. pumilio* forests, the pseudoscorpions were sensitive to harvesting, with similar abundances in harvested forests (aggregated and dispersed retentions) and grasslands. In *N. antarctica* forests, differences were not detected among unmanaged and silvopastoral managed forests, probably due to higher understory plant growth, and lesser diminishing of litter and debris by thinning than by harvesting. We conclude that the pseudoscorpion, *N. michaelseni*, can be a good bioindicator for ecosystem conservation and for evaluating recovery rate in the ecological conditions of impacted *Nothofagus* forests, and that management practice intensities should be regulated to create more suitable habitats for pseudoscorpion diversity conservation.

Keywords: South Patagonia, conservation, natural vegetation types, variable retention, silvopastoral use

Bioindicators are taxa or functional groups that can reflect the state of the environment, acting as early warning indicators of changes (environmental indicator), monitoring a specific ecosystem stress (ecological indicator) or indicating levels of taxonomic diversity (biodiversity indicator). Environmental and ecological bioindicators can be divided into several categories reflecting their responses to environmental changes: detectors (naturally occurring indicators that decrease with environmental stress), exploiters (increase with environmental stress) and accumulators (organisms that take up chemicals and can be used to measure toxin levels). Bioindicators may also be used for conservation prioritization by means of spatial comparisons of a site value, or monitoring of ecosystem recovery or response to management.

To be used as a bioindicator, a well-known distribution and environmental tolerance level of a particular taxonomic group or species are needed. Taxa at a higher level of the food chain would seem to be better indicators as they indicate processes lower in the food chain. Invertebrates may often be particularly good environmental and ecological bioindicators due to their sensitivity to local changing conditions. In turn, invertebrates usually present short generation times that result in rapid numerical responses, and variability in the ecological characteristics of some species produce a wide range of specific responses related to the environment where they live. Likewise, invertebrates may reflect trends in species richness and community composition more accurately than vertebrates, as the invertebrates are more diverse and abundant, reflect levels of overall species richness and community composition, and are more cost-effective to use. Among invertebrates, pseudoscorpions have only occasionally been used as bioindicators (Yamamoto et al. 2001; Barros et al. 2010; Ranius et al. 2011), because they are generally scarce and difficult to identify. But some studies have revealed their sensitivity to anthropogenic activities, with greatest population densities in environments with major ecological equilibrium, as in old-growth forests (Yamamoto et al. 2001).

Pseudoscorpions are one of the smaller orders of Arachnida, and sometimes occur in large numbers. Most species of pseudoscorpions live in the tropics and subtropics throughout the world (Del-Claro & Tizo-Pedroso 2009); however quite a few species live in the temperate zone. Preferred microhabitats of pseudoscorpions are leaf litter of woods and forests, crevices, nests of mammals, and logs. Only a few studies on the ecology of pseudoscorpions, habitat selection, and niche preferences have been done so far (e.g., Bell et al. 1999; Dennis et al. 2001; Derraik et al. 2001; Yamamoto et al. 2001; Tizo-Pedroso & Del-Claro 2014). There are no works about pseudoscorpions in *Nothofagus* forests of South America, although they were found in *Nothofagus truncata* litter in New Zealand (McColl 1975).

Nothofagus forests in Tierra del Fuego Archipelago are the world's southernmost forested ecosystem, and one of the last remaining pristine wilderness areas on the planet. However, there are several human-related influences that incrementally modified the original structure and natural dynamic of these ecosystems, e.g., harvesting, the presence of livestock, and the occurrence of exotic species (e.g., beaver, mink), which have

affected the entire forest system and modified biodiversity levels at understory, forest soil and canopy levels (e.g., Gustafsson et al. 2012). Silviculture focused on sustainable forest management aims to conserve biodiversity at different spatial levels. However, there is a lack of knowledge about the complete assemblage of species and their natural distribution in different ecosystems for some taxa, e.g., arachnids. This information is required to set up explicit recommendations on how to minimize impacts on natural ecosystems, mainly on endangered species (Lindenmayer et al. 2012).

We studied the distribution and abundance of a pseudoscorpion species, *Neochelanops michaelseni* (Simon 1902) (Chernetidae) (henceforth referred to as *Ne. michaelseni* to distinguish its generic name from that of the plants in the genus *Nothofagus*), in different natural *Nothofagus* forested and associated non-forested ecosystems. Also, we were interested in how this species responds to different forest uses (harvesting in *N. pumilio* forests and silvopastoral management in *N. antarctica* forests). The hypotheses tested here are: (1) *Ne. michaelseni* is differentially distributed in typical vegetation types of Tierra del Fuego, and presents greater abundance in *Nothofagus* forests than in non-forested ecosystems; (2) *Ne. michaelseni* is sensitive to environmental and ecosystem stress produced by the forest use, resulting in its reduced abundance in harvested and silvopastoral managed forests. Using this information we discuss the utility of *Ne. michaelseni* as a bioindicator of conservation status for different vegetation types in southern Patagonia.

METHODS

Southern Patagonian *Nothofagus* forests.—The austral extreme of South America, Tierra del Fuego Island, hosts the world's southernmost forested ecosystems. *Nothofagus* genus is the main component, with a wide range of natural distribution from 36°50′ to 55°02′S. These forests are predominantly deciduous, mainly composed of *N. pumilio* (NP) and *N. antarctica* (NA). In the Argentinean territory of Tierra del Fuego, forests are mainly used for harvesting, cattle grazing and tourism, prioritizing economic aspects over conservation in the ecosystem management. These *Nothofagus* forests rarely constitute large continuous masses, rather the landscape is usually formed by a mosaic of several forest types and open environments, where timber and unproductive forests are mixed.

Studied sites.—The study was conducted on long-term plots as part of the PEBANPA network (Biodiversity and Ecological long-term plots in southern Patagonia), established at Los Cerros Ranch (54°18′S, 67°49′W) and San Pablo Ranch (54°15′S, 66°49′W), within an area of 1500 ha each. The landscape is occupied by monospecific natural *Nothofagus* forests, grasslands and peatlands. Acid brown soils are mostly of glacial origin with loess and alluvial materials at the foothills. The climate is cold, with short, cool summers and long, snowy and freezing winters; the growing season extends from November to March. Mean monthly air temperatures range from -3 to 10°C (July and February, respectively), while soil temperatures vary from 0°C (August) to 9°C (March). Precipitation (rain and snow) reaches up to 600 mm yr^{-1} (Soler et al. 2012).

To study pseudoscorpion abundance in different vegetation types, we selected two unmanaged, old grown *Nothofagus* forests (NA and NP forests) and two associated non-forested ecosystems (grasslands and peatlands) in Los Cerros Ranch, covering an area of 5–10 ha each. In each vegetation type, six sampling sites were selected as spatial replicates, with similar characteristics in vegetation community composition and topography.

To analyse the pseudoscorpion responses to harvesting in NP forests, three habitat types were selected in harvested sites in Los Cerros Ranch: (i) interior of aggregated retention (AR), (ii) areas of dispersed retention (DR) in the harvested forests 20 m away from the aggregates' edges, and (iii) unharvested stands of old growth unmanaged forests (NPF), with six spatial replicates each. These sites were located on a long-term plot established in a pure NP forests (115 ha) harvested in 2005, seven years before the onset of this study. The variable retention method applied in Tierra del Fuego generates various canopy openness and micro-environmental conditions, because it retains one circular aggregate of 30 m radius per hectare (30 m^2 ha^{-1} basal area), and evenly dispersed dominant trees are retained (10–15 m^2 ha^{-1} basal area) between the aggregates. The studied stands were of middle-to-high site quality, with a total overbark volume of 700–900 m^3 ha^{-1}, total dominant heights of 20.5–27.5 m and basal area of 60 m^2 ha^{-1} (Martínez Pastur et al. 2011).

To analyse the pseudoscorpion responses to silvopastoral use in NA forests, two habitat types were selected in managed stands in Los Cerros Ranch (four spatial replicates of each habitat) and San Pablo Ranch (six spatial replicates of each habitat): (i) silvopastoral managed forests (SF), and (ii) unmanaged old growth stands (NAF). Silvopastoral managed forests had mature trees (130–180 years old) that had been handled by selective cutting and thinning (reducing 50% of the original cover) about 7–10 years before the onset of this study (Soler et al. 2012). This canopy management improved the understory biomass (annual increase of 1400 kg ha^{-1} of dry matter), which is used as forage for cattle grazing. The old growth unmanaged forests correspond to 150–200 years old stands without forestry intervention, whose forest structure (large trees, multilayered canopy, and big coarse woody debris) is the result of natural disturbances (e.g., wind throws). Livestock carrying capacity in both ranches is about 7–8 individuals km^{-2} (cattle), mainly of Hereford breed. The traditional grazing management is based on extensive winter and summer grazing paddocks (400–1000 ha approximately), where each paddock includes mixed habitat types (NA forests, grasslands, and peatlands). Cattle graze on grasslands during summer-autumn, but they also use *Nothofagus* forests in winter-spring. In this region, natural populations of guanaco (*Lama guanicoe*) occur, meaning that native and domestic herbivores overlap in the use of grasslands and forests habitats for feeding and shelter.

Pseudoscorpion sampling.—Because pseudoscorpions live primarily in litter, sampling was performed by means of pitfall traps, which mainly reflects the activity of animals walking on the soil or leaf litter surface, but was previously used for pseudoscorpion sampling (e.g., Derraik et al. 2001). In these studies, pitfall traps had two different designs. (A) in vegetation types and NP forests, at Los Cerros ranch, we

used a laterally opened cylinder (100 cm long × 15 cm diameter) placed horizontally in each site. Traps were emptied every 15 days during one summer season (six sampling periods from December 21st to March 21st, 2013, counted as days after the beginning of the study: 15, 30, 45, 60, 75 and 90 days). And (B) in NA forests, both at Los Cerros and San Pablo ranches, five plastic pots (12 cm height × 14 cm diameter) were set up 5 m apart from each other in a cross design. Pots were open during 7 days at the end of January 2013. The growing season period (November-April) was considered appropriate for arthropod sampling in *Nothofagus* forests at Tierra del Fuego due to higher temperature. Water was used as a retention agent and a few drops of commercial detergent were employed to diminish surface tension.

After trapping, individuals were identified to species level using external morphology and linear measures (Mahnert et al. 2011) as well as the spermatheca shape (Mahnert 2001), and classified by sex–age into classes (adult male and female, proto-, deutero-, and tritonymph). Because of the small number of nymphs, all nymphal stages were regrouped in the class juveniles for analysis. Almost all individuals belonged to the species *Ne. michaelseni*; only four individuals belonged to another species (from the genus *Serianus* Chamberlin 1930), and they were excluded from the analyses. The samples are deposited in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina.

Data analyses.—We used different ANOVA models to evaluate the abundance of *Ne. michaelseni* (response variable) in the sampling period. Data were square root transformed to accomplish ANOVA assumptions of homoscedasticity, but non-transformed means are presented to improve interpretation. In all analyses, means were compared by the Tukey honestly significant difference test ($p < 0.05$).

To investigate differences in abundance of *Ne. michaelseni* among vegetations types and harvesting regimes in NP forests we used repeated measures ANOVAs (with spatial and temporal replications). Days after the beginning of the study was the repeated factor, while vegetation types ($n = 4 \times 6 \times 6 = 144$) and harvesting regimes ($n = 3 \times 6 \times 6 = 108$) were the main factors. When the sphericity test was significant in repeated measures ANOVAs, a univariate adjustment was applied to evaluate within-subjects effects (Greenhouse & Geisser 1959). As interactions occur in both repeated measures ANOVAs, the impact of one factor depends on the level of the other factor. Therefore, one-way ANOVAs were performed to evaluate differences in *Ne. michaelseni* abundance among treatments (vegetation types and harvesting regimes) for each day after the beginning of the study, and among days after the beginning of the study for each treatment.

Moreover, we used two-way ANOVA to investigate the impact of silvopastoral management in NA forests (spatial replication), using habitat type and ranch as main factors ($n = (2 \times 4) + (2 \times 6) = 20$). Subsequently, multivariate cluster analysis was done for each data set to reveal ecological relationships between ecosystems and managed forests, using Euclidean distance and Ward's method. Statistica (Statsoft, USA) and Statgraphics (Statistical Graphics Corp., USA) software was used for these analyzes.

RESULTS

There were 812 individuals of *Ne. michaelseni* sampled, 718 by opened cylinders during the whole summer season, and 94 by pots during seven days in January. From these, there were 453 males, 308 females and 51 juveniles. The highest quantities of males and females occurred 30 days after the beginning of the study (89 and 62 individuals, respectively), while juveniles presented the greatest abundance 15 days after sampling began (13 individuals). Sex–age classes presented similar proportions in both trap designs (56% males, 38% females and 6% juveniles in opened cylinders, and 52% males, 40% females and 7% juveniles in pots).

Pseudoscorpion abundance differed among natural vegetation types (Repeated-measures ANOVA, $F = 7.80$, $P = 0.001$) and days after the beginning of the study (Repeated-measures ANOVA, $F = 23.95$, $P < 0.001$), although interaction was significant (Repeated-measures ANOVA, $F = 2.57$, $P = 0.014$) due to very low abundances at 60 days after the beginning of the study in all vegetation types, and in grasslands during the whole season. Complementary analyses revealed abundance was significantly higher in NA forest and lower in grasslands in five sampling periods (Table 1). NP forest abundance did not show differences with NA forests 30 days after the beginning of the study, while peatlands were significantly similar to grasslands 45, 75 and 90 days after the beginning of the study (Table 1). On the other hand, peatlands, NA and NP forests presented significantly higher abundances 30 days after the beginning of the study (Repeated-measures ANOVA, $F = 7.84$, $P < 0.001$ for peatlands; $F = 3.88$, $P = 0.008$ for NA forests; $F = 3.09$, $P = 0.023$ for NP forests), which was also high in NA forests at 15 days after the beginning of the study (Fig. 1a). Likewise, peatlands and grasslands had significantly lower abundances from 45 days after the beginning of the study until the end of the sampling period, except in NP forest which incremented at 90 days after the beginning of the study. Abundance was minimal and differences were not detected for grasslands (Fig. 1a).

On the other hand, pseudoscorpion abundance differed among NP harvested and unharvested forests (Repeated-measures ANOVA, $F = 11.89$, $P = 0.004$) and days after the beginning of the study (Repeated-measures ANOVA, $F = 5.36$, $P < 0.001$), but interaction was significant (Repeated-measures ANOVA, $F = 5.20$, $P < 0.001$) due to very low abundances in AR and DR during the whole season. Complementary analyses confirmed significant differences among NP harvesting regimes 30, 60 and 90 days after the beginning of the study, with greater values in NPF than in AR and DR (Table 1). Likewise, significant differences were found among days after the beginning of the study only for NP unharvested forests (Repeated-measures ANOVA, $F = 3.09$, $P = 0.023$), where abundance of *Ne. michaelseni* was significantly higher at 30 days than at 45, 60 and 75 days after the beginning of the study, with intermediate values for 15 and 90 days (Fig. 1b).

In NA forests, significant differences in pseudoescorpion abundances were not detected between unmanaged and silvopastoral managed forests (Repeated-measures ANOVA, $F = 1.99$, $P = 0.177$), with the average abundance of 4.7 individuals *per* sampling unit. Likewise, significant differences were not detected between ranches (Repeated-measures

Table 1.—One-way ANOVA and Tukey test results for *Ne. michaelseni* abundance comparing different vegetation types and NP harvested and unharvested forests, at 15-day intervals after the beginning of the study. NAF = old growth NA forests; NPF = old growth NP forests; AR = aggregated retention in NP forests, DR = dispersed retention in NP forests.

Terms and factor levels	Days after the beginning of the study					
	15	30	45	60	75	90
Vegetation types						
NAF	10.7 b	11.5 b	3.7 b	1.3	2.3 b	4.3 b
NPF	3.3 ab	9.7 b	1.5 ab	0.5	0.8 ab	1.7 ab
Peatlands	1.7 ab	3.5 ab	0.2 a	0	0.0 a	0.0 a
Grasslands	0.3 a	0.5 a	0.2 a	0	0.0 a	0.2 a
F (*p*)	5.28 (0.008)	6.37 (0.003)	4.92 (0.010)	3.01 (0.054)	8.65 (<0.001)	5.86 (0.005)
Habitat types						
NPF	3.3	9.7 b	1.5	0.5 b	0.8	1.7 b
AR	0.2	0.2 a	0.5	0.0 a	0.2	0.0 a
DR	0.3	0.3 a	0.3	0.0 a	0.2	0.0 a
F (*p*)	1.84 (0.194)	12.18 (<0.001)	0.36 (0.707)	5.00 (0.022)	1.43 (0.270)	6.71 (0.008)

ANOVA, $F = 3.81$, $P = 0.069$), which had 4.4 individuals on average *per* sampling unit. Moreover, interactions were not significant in this analysis (Repeated-measures ANOVA, $F = 0.35$, $P = 0.561$).

Cluster analyses highlighted the similarities among *Ne. michaelseni* abundance in NP and NA forests compared to grassland and peatlands (Fig. 2a). Correspondingly, there were similarities in aggregated and dispersed retention harvesting compared to unharvested NP forests (Fig. 2b), and between unmanaged NA forests from Los Cerros and San Pablo Ranches compared with sivopastoral managed sites (Fig. 2c).

DISCUSSION

Neochelanops michaelseni was the main pseudoscorpion species detected in central Tierra del Fuego forests and non-woody habitats. This species is the only native cited for Tierra del Fuego (Mahnert et al. 2011) and its habitat preferences are practically unknown. The other species recorded for Tierra del Fuego is *Chelifer cancroides* (Linnaeus 1758), which might have been introduced during colonial times, and has not been recorded in Argentina since 1905 (Mahnert et al. 2011). On the other hand, the other pseudoscorpion species detected in this study, *Seriatus* sp., was not previously found in Tierra del Fuego.

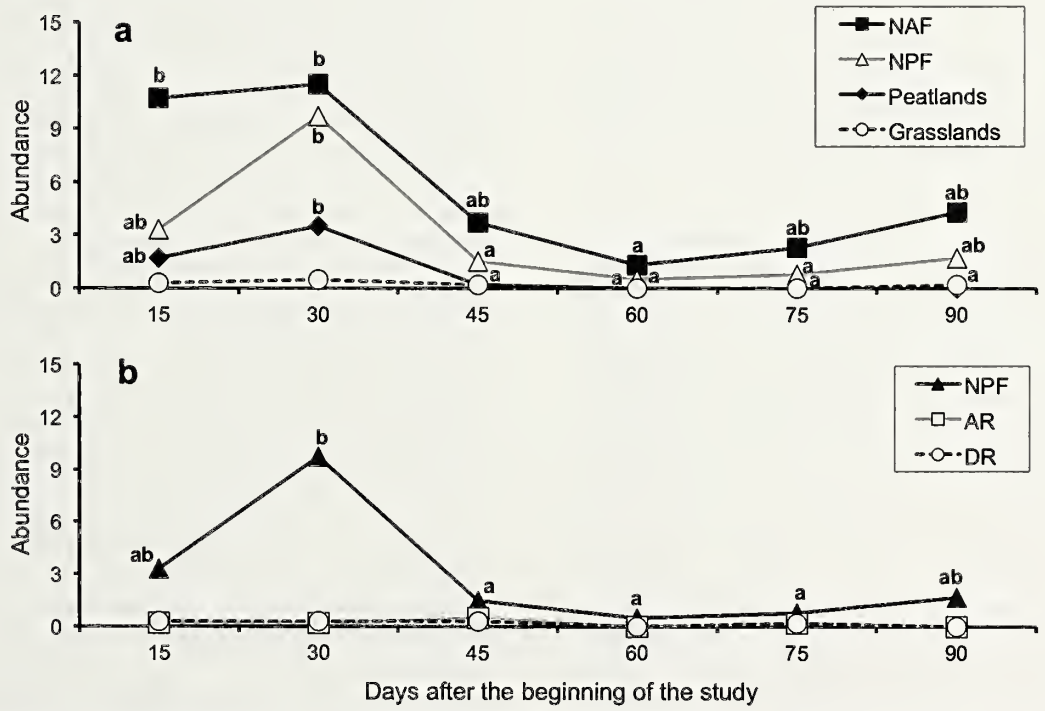

Figure 1.—Changes in mean abundance of *Ne. michaelseni* during the course of study for (a) different vegetation types, considering old growth NA forests (NAF), old growth NP forests (NPF), peatlands and grasslands, and (b) different harvesting regimes in NP forests, considering unharvested old growth (NPF), aggregated retention (AR) and dispersed retention (DR) forests. Letters corresponded to differences by Tukey test at $p < 0.05$.

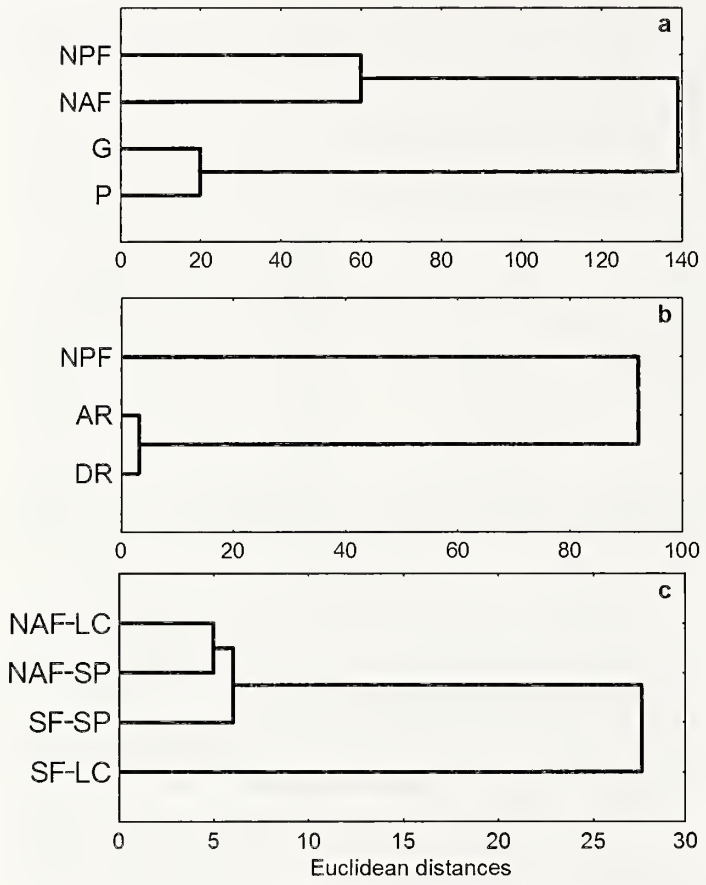

Figure 2.—Cluster analysis for *Ne. michaelseni* abundance in Tierra del Fuego, corresponding to: (a) different vegetation types, considering old growth NP forests (NPF), old growth NA forests (NAF), grasslands (G) and peatlands (P); (b) different harvesting regimes in NP forests, considering unharvested old growth (NPF), aggregated retention (AR) and dispersed retention (DR) forests; and (c) silvopastoral management in NA forests, considering unmanaged old growth forests in Los Cerros Ranch (NAF-LC) and San Pablo Ranch (NAF-SP) and silvopastoral managed forests in Los Cerros Ranch (SF-LC) and San Pablo Ranch (SF-SP).

Our study highlights the dissimilar abundance of *Ne. michaelseni* among typical vegetation types of Tierra del Fuego landscape, with greatest abundances in woodlands and relatively low abundance in grasslands and peatlands. Leaf litter is the ancestral habitat of pseudoscorpions, which provides an ideal stable environment (Jones 1970), and encloses a specific litter fauna that plays a very important role in the transformation of leaf litter into humus. Pseudoscorpions are at the upper level of this trophic chain, feeding on primary or secondary herbivores, such as mites, collembolans, nematodes, woodlice, millipeds, insects, and earthworms (Buddle 2005). Litter in forests could provide a more stable and richer environment than litter in grasslands and peatlands, which could explain the higher abundance of *Ne. michaelseni* in woody vegetation types. Although a few authors have examined pseudoscorpion diversity in grasslands and other open environments around the world (Rapp 1978; Bell et al. 1999; Dennis et al. 2001), more studies are needed to explore pseudoscorpions in non-woody vegetation types.

On the other hand, pseudoscorpions of the family Chernetidae are often found in hollow stumps and hollow trees (Snow 1958; Ranius & Wilander 2000), but also under the bark of trees and logs (Buddle 2005), in leaf litter adjacent to fallen logs (Hoff 1949), and in the wood of 10 and 20 years old stumps (without hollows) (Persson et al. 2013). Indeed, some species of Chernetidae had clearly higher abundances in bark and wood than in soil or litter (Persson et al. 2013). Therefore, higher abundance of *Ne. michaelseni* in woodlands than in grasslands and peatlands could be related to the presence of coarse woody debris, logs and stumps at different stages of decomposition, usually found in the floor of old growth *Nothofagus* forests (Lencinas et al. 2008, 2011), which could be the typical microhabitat of this species.

Beside differenees among vegetation types, *Ne. michaelseni* abundance was highest in old-growth forests compared to managed or harvested stands, as was observed by Yamamoto et al. (2001) and Burghouts et al. (1992) in other forests. Disturbances affect pseudoscorpion abundance, likely due to changes in the availability of microhabitats. The reduction of canopy cover by harvesting in the original NP forest structure negatively impacts the amount of leaf litter that reaches the forest floor in harvested sites (Martínez Pastur et al. 2008), which may lead to the decrease of pseudoscorpion populations. On the other hand, variable retention harvesting in NP forest increased debris cover and biomass compared to old growth forests (Lencinas et al. 2011), mainly medium size debris and small branches (Martínez Pastur et al. 2011). Recently generated large debris probably needs time to start rooting and constitute appropriate habitats for pseudoscorpions. Because this study was performed in stands harvested seven years ago, more studies must be carried out in older harvested sites, with coarse woody debris at different stages of decay. Additionally, harvesting greatly modifies microclimate below NP canopy (Promis et al. 2010), which could generate dramatic fluctuations in the humidity and temperature regimes, with a potential negative impact on decomposition rates (Frangi et al. 1997) and pseudoscorpion abundance, even if they inhabit coarse woody debris. Timing and intensity of management may have a significant impact on the abundance of pseudoscorpions too (Bell et al. 1999).

Variable retention harvesting, a stand-level conservation approach to better integrate woody production and biodiversity conservation (Gustafsson et al. 2012), is proposed for south Patagonian forests, and applied as well in Europe, North America, Latin America, and Australia. In NP forests, variable retention was useful to improve conservation of biodiversity and natural cycles in the managed forests (e.g., Lencinas et al. 2011, 2012), mainly inside aggregates. However, similar *Ne. michaelseni* abundances were found inside and outside aggregates at least seven years after harvesting, with comparable values to grasslands. The recovery of forest structure in secondary forests may also allow recovery of pseudoscorpion populations, probably due to deeper litter build-up over time. The longer the secondary forest has to develop, the more stable and ultimately more suitable the litter environment becomes (Jones 1970).

On the other hand, *Ne. michaelseni* abundance did not differ significantly between silvopastoral managed and unmanaged NA forests, probably because thinning did not greatly affect

litter production or debris abundance in this system. Differences among *Nothofagus* forests must be considered, because NA forests constitute open woodland, with richer and more productive understory than NP forests (Lencinas et al. 2008). Under silvopastoral management, decrease of litter production could be also produced by livestock consumption of herbaceous plants and trampling. Additionally, thinning increases radiation at the understory level, which stimulates grass biomass production. Therefore, litter reduction is less in silvopastoral managed NA than in harvested NP forests, which could generate less impact in pseudoscorpion populations. Since Dennis et al. (2001) found abundance of pseudoscorpions to be greater in ungrazed and taller grazed swards than in short grazed swards, and Rapp (1978) determined that grazing caused a decline in the number of pseudoscorpions because of adverse changes in soil moisture and litter depth, more studies are necessary to evaluate the impact of contrasting silvopastoral management intensities in NA forests.

All sex-age classes (male, female and juveniles) of *Ne. michaelseni* were more abundant at the beginning of the sampling period (early summer). This could be related to temperature, because many species of pseudoscorpions are active throughout spring, summer, and autumn and hibernate during winter, with juveniles emerging in spring. In Tierra del Fuego, the abbreviated growing season could accelerate these processes. Precise information about the life cycles of pseudoscorpions depends on quantitative sampling over a period of years. Therefore, the present work enriches the knowledge about this almost unknown species, and offers tools for better planning of the sampling.

This study highlights the feasibility of *Ne. michaelseni* as a bioindicator for ecosystem conservation, mainly in NP forests, and generates useful and necessary information related to their presence in typical vegetation types in south Patagonian forests. Due to their small size, pseudoscorpions' ability to disperse to other environments is limited (Zeh & Zeh 1992; Del-Claro & Tizo-Pedroso 2009). Consequently, we conclude that *Ne. michaelseni* is a good detector of forest disturbances, and could be used to evaluate the recovery rate in the ecological characteristics of impacted *Nothofagus* forests. Similarly, other pseudoscorpion species were sensitive to management showing dissimilar abundances under different managements (Burghouts et al. 1992; Bell et al. 1999; Yamamoto et al. 2001; Barros et al. 2010) and in grasslands where pseudoscorpions are not abundant. Management practice intensities (mainly harvesting) should be regulated to create more suitable habitats for pseudoscorpion diversity conservation.

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SHORT COMMUNICATION

Day-time vs. night-time sampling does not affect estimates of spider diversity across a land use gradient in the Neotropics

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Abstract. To obtain a reliable description of spider communities, robust sampling protocols are crucial. However, it remains unclear if descriptions of spider communities in tropical habitats require both day and night sampling. Here we tested whether sampling both day and night in high and low vegetation strata would lead to better diversity estimates of spider communities than sampling at only one period of the day. We determined spider taxonomic diversity in a network of 12 plots in French Guiana along a vegetation gradient. We found high alpha diversity of spiders as expected for a tropical area at every site. We showed strong differences in spider alpha and beta diversity between high and low vegetation strata, while they were similar between day and night sampling. Our results suggest that collecting spiders at only one period is sufficient to describe the diversity of spider communities across land use types in the neotropics.

Keywords: Araneae, community, sampling protocol, night, day

An essential first step towards a better understanding of arthropod communities is a reliable description of community composition and abundance via a robust sampling protocol. Sampling needs to represent accurately the target group and also to optimize the ratio of data quality to sampling effort. However, although a common sampling protocol is beginning to be globally used (Cardoso 2009), some parameters still need to be tested and improved.

Spiders inhabit almost every terrestrial habitat (Cardoso et al. 2009). They have developed various hunting strategies (e.g., ambushing, wandering, web building, door trapping) in order to hunt efficiently and to minimize interspecific competition (Cardoso et al. 2011). This variety of feeding behaviors increases the difficulty of sampling the whole spider community entirely and precisely. To cover such wide spatial and temporal activities, several sampling protocols combining passive and active techniques have been established to optimize sampling effort in space and time (Coddington et al. 1991, 2009; Cardoso 2009; Vedel et al. 2011; Vedel & Lalagüe 2013). To examine the spatial distribution of spiders, one of the parameters is to study strata. Some sampling techniques are specifically used to collect spiders from a vegetation stratum. The most efficient techniques, commonly used on boreal forest and Mediterranean habitats, are the pitfall traps and nocturnal hand collecting for leaf litter, the sweep net for lower understory vegetation and the beating tray for higher understory vegetation (Vedel & Lalagüe 2013). In addition to spatial distribution, the time of sampling may represent an essential factor for sampling spider communities (Coddington et al. 1991; Sorensen et al. 2002; Cardoso et al. 2008, 2009). Indeed, most spiders are active only at night, while a smaller community is active only during the day, and an even smaller proportion is active during both periods (Foelix 2013). It has thus been argued that sampling has to be conducted both day and night to capture spiders with both diurnal and nocturnal activities (Cardoso et al. 2009; Vedel & Lalagüe 2013). Spider species inhabiting the leaf litter are foraging during their active period (very often at night) and are hiding in burrows to rest. Some sampling methods (e.g., pitfall traps and nocturnal hand collecting) ean catch them only when they are in their active period out of their burrow. In understory vegetation layers, where more than the three quarters of spider species found in tropical habitats live (Coddington et al. 2009), spiders forage and rest on the same habitat, on the vegetation. Nevertheless, it remains unclear whether diurnal and nocturnal sampling is necessary to characterize the hyperdiverse tropical arachnid communities.

Here we aimed at assessing whether sampling both day and night with multiple methods would lead to better estimates of spider community diversity than sampling at only one period of the day across vegetation strata along a gradient of land use in French Guiana. We expected to find that, to acquire meaningful measures of spider diversity, it is not necessary to sample both during the day and at night in the understory vegetation of tropical forests.

We established a network of 12 plots within a 20-km^2 area along the road Degrade Saramaka, near Kourou, in French Guiana. Local climate is typically equatorial with a rather constant temperature across the year around 26°C and with high humidity divided into two main seasons: one with high precipitation from December until June and the other with little precipitation from July to November.

Three 50 m x 50 m plots were located in each of four land-use types. Each plot from one land-use type had similar vegetation communities. These four land types therefore represented a gradient of vegetation from higher cover to lower cover of vegetation, respectively: (i) undisturbed tropical forest, (ii) forest edge, (iii) agricultural land after slash and burn, and (iv) garden.

We used the optimized and standardized protocol originally established by the widely used COBRA protocol for arthropods (Cardoso 2009; Cardoso et al. 2009), and further adapted to tropical rain forests (Vedel & Lalagüe 2013). Spiders were sampled at two vegetation strata: high understory (tree samplings) using beating trays, and low understory (grasses, forbs, shrubs and tree seedlings) using sweeping nets during two periods: day time (0800–1200) and night time (2100–2400). The sampling effort was of one hour per technique per day period per plot (four hours on each plot). Sampling was conducted 15–29 July 2013, i.e., during the end of the raining season.

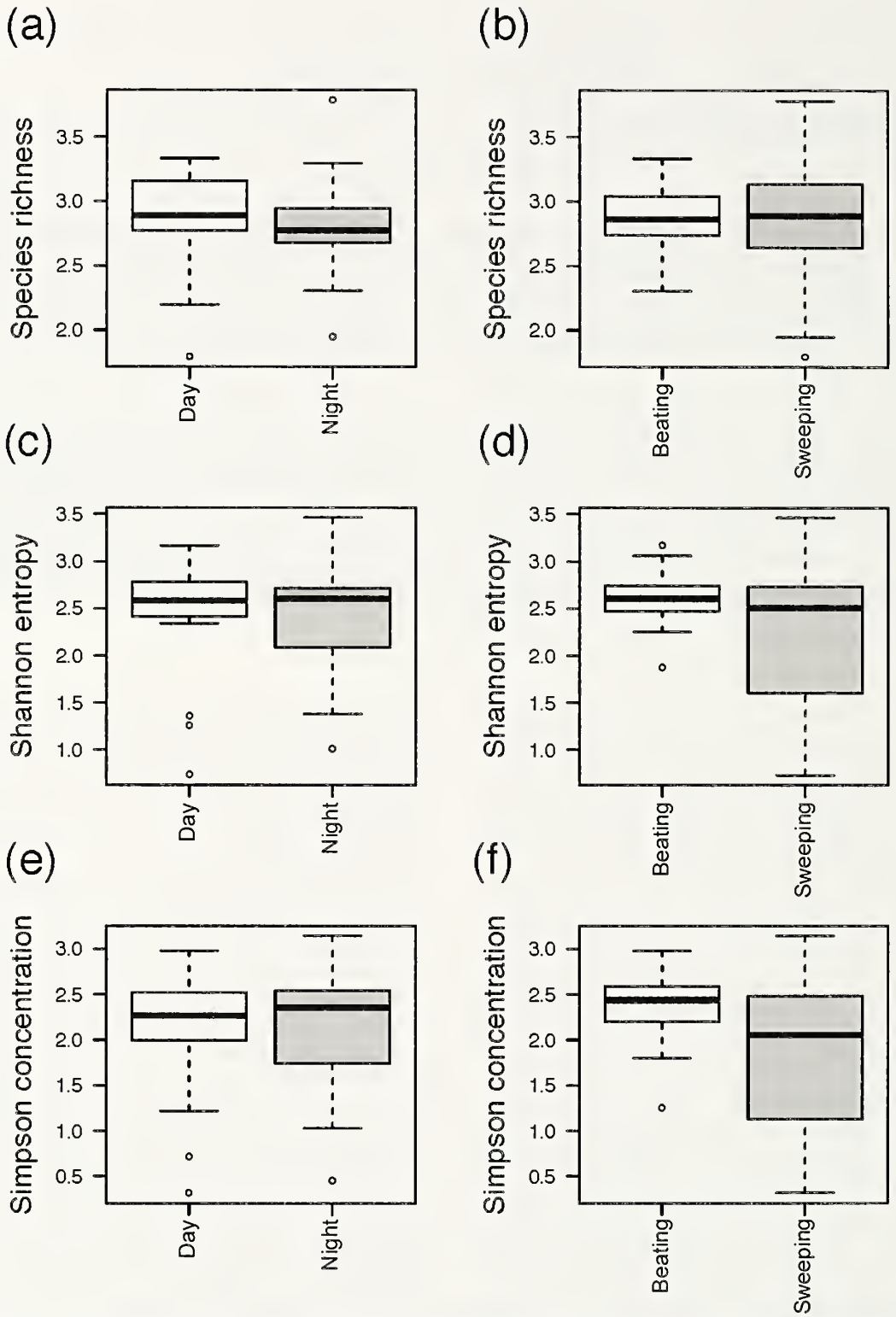

Figure 1.—Boxplots of species richness (a, b), Shannon entropy (c, d) and Simpson concentration (e, f) by sampling time and vegetation strata.

Samples were placed in tubes filled with ethanol (70%) and labeled after sampling technique (beating, sweeping) and period of the day (day, night) in each plot. For each sample, we sorted and identified individual spiders at the species level, defining morpho-species (M-S) only when there was no matching species in the literature (Brescovit et al. 2002; Levi 2002; Proszynski 2007; Vedel et al. 2013). If juvenile spiders were old enough to be identified at the species level, we included them. No M-S was defined by only juveniles. We collected a total of 2292 individuals belonging to 39 families, 100 genera and 414 morpho-species. Following the classification described in Cardoso et al. (2011), each species was assigned to a functional guild relating to feeding behavior.

We used rarefaction curves to assess species richness from the results of sampling. We characterized the alpha diversity of spider

Table 1.—Influence of sampling period and vegetation strata on spider alpha diversity. *F* statistics are shown with significance test (**: $P < 0.01$; *: $P < 0.05$; ns: not signifieant).

	Daytime		Vegetation strata		Daytime X vegetation strata	
Species richness	0.493	ns	0.445	ns	1.292	ns
Shannon entropy	0.132	ns	5.433	*	0.513	ns
Simpson concentration	0.021	ns	7.339	**	7.339	ns

communities as (i) species richness, (ii) Shannon entropy and (iii) Simpson concentration (Jost 2007). We determined the beta diversity of spider communities as distance matrices of taxonomic compositions using the Bray-Curtis metrics, calculated (i) with species presence-absence and (ii) with species abundances (Legendre & De Cáceres 2013).

To test the effect of sampling time (day/night), vegetation strata (high/low understory) and their interaction on spider taxonomic alpha diversity, we used three-way analysis of variance (ANOVA). To test the effect of sampling time and vegetation strata on spider taxonomic beta diversity, we conducted a permutational multivariate analysis of variance for partitioning distance matrices between the two sources of variation.

All analyses were conducted in the R 3.0.2 statistical platform (R Development Core Team 2011), using the package vegan (Dixon 2003).

We found a high alpha taxonomic diversity of spider species in every habitat and stratum. For comparison, here 414 M-S were identified for 2292 individuals collected (intensity = 5.54) while the averages of other tropical sites (reviewed in Coddington et al. 2009) are 303.75 M-S for 3170.8 individuals sampled (intensity = 10.45). In boreal white spruce stands, 3070 specimens were collected representing 76 species (intensity = 40.40). Because different sampling protocols and indices were used for the earlier studies, their indices are comparable to ours only in that they suggest the high species richness of the sites we sampled.

We also found no variation in spider alpha diversity between sampling times and no interaction between sampling time and vegetation strata (Table 1, Fig. 1a, c, e). Although we found no change in species richness between vegetation strata, we showed that Shannon entropy and Simpson concentration were higher in the high understory than in low understory (Fig. 1b, d, f).

Table 2.—Influence of sampling period and vegetation strata on spider beta diversity, calculated for species presence-absence and for species abundances. *F* statistics are shown with significance test (***: $P < 0.001$; *: $P < 0.05$; ns: not significant).

	Daytime		Vegetation strata	
Beta diversity:				
Species presence-absence	1.0834	ns	2.4051	***
Species abundance	1.1791	ns	1.5505	*

We showed no influence of sampling time on spider beta diversity, calculated without and with species abundances (Table 2). However we found a strong effect of vegetation strata in spider beta diversity, calculated without and with species abundances (Table 2). This confirms that it is essential to consistently use both sampling methods (sweeping and beating) to capture the spider diversity in the two vegetation strata (Cardoso et al. 2009; Vedel & Lalagüe 2013). Figure 2 illustrates that low and high understories form two different clusters, with species abundances and with species presence-absence. Spider beta diversity was thus more similar within vegetation strata of the 12 plots than between vegetation strata of one plot.

The lack of differences in spider alpha and beta diversity during day or night sampling suggests that collecting spiders at only one time during the day appears to be sufficient to describe the diversity of spider communities across vegetation types in this area in the Neotropics.

Our findings confirm the only two studies using similar experimental designs, where vegetation strata were separated and where the leaf litter stratum was not included, though they were performed in temperate forests (Coddington et al. 1996; Dobyns 1997). In contrast, studies finding an opposite result from ours used generally another experimental or analytical design, therefore making a comparison of the final results difficult. Coddington et al. (1991) found differences between day and night sampling, but collecting techniques including leaf litter sampling were not separated, which biases the overall results. Also respectively in temperate and in tropical habitats, two other studies show the same results as Coddington et al. (1991) but also did not separate sampling techniques for the soil and the vegetation (Green 1999; Sorensen et al. 2002). Finally, in Mediterranean habitats, results are also ambiguous. Beta-diversity varied depending on the statistical

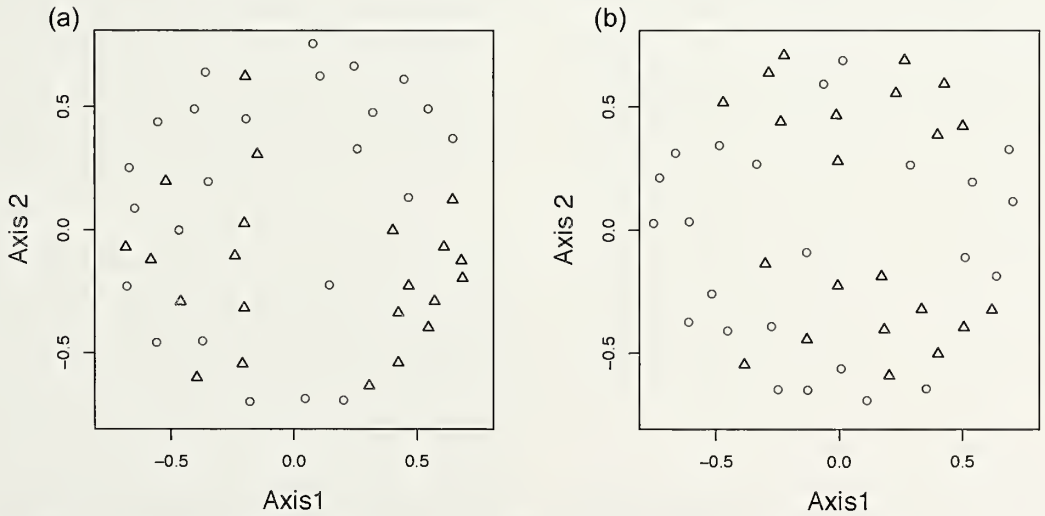

Figure 2.—Taxonomic beta similarity between vegetation strata based on species abundance (a) and based on species presence-absence (b), plotted on the two main axes determined by non-metric multidimensional scaling. Circles stand for high understory, and triangles stand for low understory.

test applied: the Spearman correlation did not find any differences between day and night sampling although the Anosim analysis did (Cardoso et al. 2008). A third study found no difference between day and night sampling for the beating techniques but a richer community of spiders collected by sweeping during night time (Cardoso et al. 2008). This supports the need for further tests to assess the generality of our findings in other ecosystems.

To optimize sampling, we thus recommend sampling spiders on vegetation at different strata by using these two techniques (sweeping lower understory vegetation and beating higher understory vegetation) at night, where the sampling of the leaf litter is efficient (data not shown).

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SHORT COMMUNICATION

How *Micrathena duodecimspinosa* (Araneae: Araneidae) uses the elasticity of her dragline to hide her egg sac

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Abstract. A female *Micrathena duodecimspinosa* (O. P. Cambridge, 1890) used the elasticity of her long dragline to repeatedly jerk her newly constructed egg sac up and down as she lowered it into the leaf litter below. Jerking may reduce the chances that the sac will be entangled in vegetation before it reaches the leaf litter or help insert it deeper into the litter, where it is visually camouflaged.

Keywords: Camouflage, oviposition, orb weaver

The eggs of spiders are attacked by a variety of enemies, including other spiders, inseets, birds, and mammals (Robinson & Robinson 1976; Austin 1985; Hieber 1992). Spiders' defenses against these dangers include physical protection by covering the eggs with silk (e.g., Gheysens et al. 2005) or with other materials such as leaves or soil (Austin 1985; Moya et al. 2010; Suter et al. 2011). This note describes a hitherto undescribed technique that the araneid *Micrathena duodecimspinosa* (O. P. Cambridge, 1890), used to insert a package containing her eggs into the leaf litter on the forest floor, and that resembles the behavior of the congeneric *Micrathena* sp. (Moya et al. 2010).

At 08:15 on 15 August 2011, I found a female *M. duodecimspinosa* in second growth near San Antonio de Escazu, San José Province, Costa Rica (el. 1325 m) resting on an egg sac that was enclosed in a tightly folded brown leaf and that hung at the end of a single suspension line about 50 cm above the ground. This line was attached about 3–4 m above the ground, and had 3–5 small white accumulations of loose silk attached to it. The folded leaf formed a nearly rectangular package (Fig. 1) that was approximately lenticular when seen from the side. I grasped the suspension line about 2 m above the ground, and carried the line, the spider and the leaf indoors to photograph them, and then taped the suspension line to a leaf outdoors about 2 m above the ground and watched the spider's behavior. The spider spent most of the next 30 min walking over the egg sac, presumably laying additional lines. Then at about 08:50 she climbed about 30 cm up the line above the sac, broke the line and attached her dragline to the line above, and began to descend slowly. Facing downward and holding the line to the sac with her anterior legs, she slowly released additional dragline, descending 30–40 cm in about 30–60 s. The sac descended all the way to the ground without snagging, and came to rest on the upper side of a weakly sloping dead leaf on the ground.

The spider then "snapped" the line 10–20 times, apparently utilizing the elasticity of the line above to reposition her sac. Each snap was apparently produced as follows. The spider gathered in line leading to the egg sac below with her anterior legs while holding the line above her with her legs IV. She moved downward approximately 1–3 cm as she reeled in line, partially lifting the sac from where it rested on the substrate below. Then she suddenly released the loose accumulation of line, and her body suddenly sprang upward about 1–3 cm. This movement of her body generally also caused the egg sac to jerk upward briefly and then fall back; generally the jerk lifted the sac only partially off the substrate. At least two of these jerks caused the sac to slide farther downward, and it finally ended up in small groove in the litter at the lower edge of the leaf where it had originally rested. The spider gradually approached the sac between the snaps, and finally contacted a curled leaf near the sac when she was only 1–2 cm above the ground. She then cut the line to the sac and decamped, climbing up the line to the leaf above, where she rested immobile.

The elasticity of the suspension line probably provided the force that produced the upward movements of the spider and her sac when she snapped the line. The reeling-in behavior must have increased the tension on the line both above and below the spider. The much longer length of the line above the spider would make it much more extensible than the line below her, so this could explain why her body descended as she reeled in line. When she released the accumulated silk, the line above would then have contracted much more than the line below because of its elasticity, thus causing the spider to be displaced rapidly upward. The upward momentum of the spider's body would in turn tense the line running downward to the sac, and because it was much less extensible, the sac would have been jerked upward.

The line snapping behavior in this species is very similar to behavior described in *Pozonia nigroventris* (Bryant 1936) and *Micrathena* sp. as they lowered their egg sacs (also wrapped in dead leaves) into the leaf litter (Moya et al. 2010). That study speculated that these manipulations of egg sacs serve to insert them deeper into the leaf litter. I propose that another and perhaps the principal function of the manipulations in these species is to avoid the egg sac becoming hung up on objects such as leaves or stems as the spider lowers the sac to the ground. The spider's poor vision (and the fact that some sacs are lowered at night) would make it difficult for her to see whether or not the egg sac had reached the ground. The visual camouflage against predators such as birds that results from being wrapped in a dead leaf would presumably be less effective if the sac were snagged on a leaf or twig above the ground.

The mechanism by which the sac was jerked upward was clearer in *M. duodecimspinosa* than in the other species, probably in part because the spider repeated the snaps so many times, and perhaps also because I anticipated that the spider might manipulate the sac and was ready to observe her behavior carefully. It is not clear whether the "vertical shakes" described for the other species also depended on the elasticity of the suspension line, but the brisk nature of these shakes (W. Eberhard unpub.) makes this seem likely.

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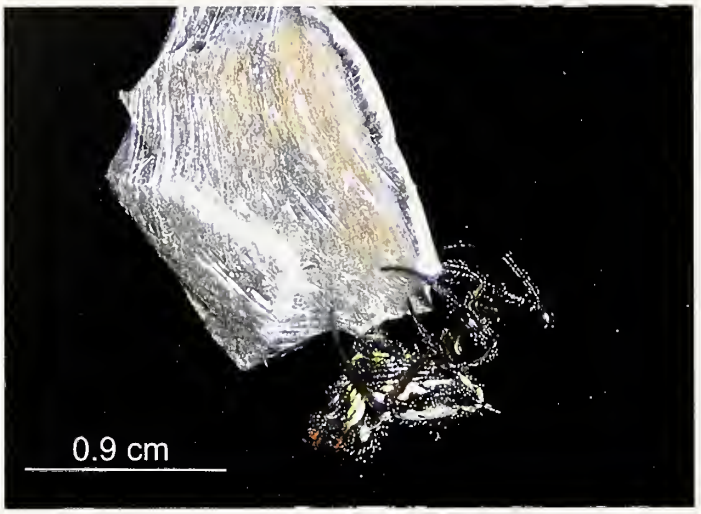

Figure 1.—A depleted female *Micrathena duodecimspinosa* rests under a tightly folded dead leaf which encloses her newly constructed egg sac.

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SHORT COMMUNICATION

New observations on a neotropical termite-hunting theridiid spider: opportunistic nest raiding, prey storage, and ceratopogonid kleptoparasites

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Abstract. A neotropical spider in the genus *Janula* Strand 1932 is reported as an opportunistic raider in damaged carton nests of the arboreal termite *Nasutitermes ephratae*. These spiders were shown to be attracted to ruptured nests and galleries from which they gather soldier termite prey that they bundle into silk-wrapped balls before suspending them away from the nests. Three species of *Forcipomyia* and one species of *Atrichopogon* (Ceratopogonidae, biting midges), rare associates of spiders, are reported as kleptoparasites on the dangling and immobilized termites.

Keywords: Theridiidae, *Janula*, Ceratopogonidae, *Nasutitermes*, spider foraging, kleptoparasitism, *Forcipomyia*, *Atrichopogon*

During a 2009 undergraduate field course in eastern Ecuador, we deliberately punctured arboreal carton nests of the termite *Nasutitermes ephratae* Holmgren in order to demonstrate how some specialized Reduviidae routinely prey on termites when nests are damaged. As expected (McMahan 1982), termite-hunting assassin bugs (*Salyavata variegata* Amyot & Serville) appeared at the damaged nests, but so did some remarkably specialized theridiid spiders of the genus *Janula* Strand 1932 (identified as *Janula* sp. near *J. erythrophthalma* (Simon 1894), previously in *Episinus* Walckenaer in Latreille 1809, see World Spider Catalog (2015)). *Janula* is close to *Episinus*, where it was formerly placed, and *Janula* plus *Episinus* may be the sister lineage of *Chrosiothes* Simon 1894 (Duran-Barron et al. 2013). The biology of the genus *Janula* was previously poorly known.

Spider specialization on termites is very rare (Pekár & Toft 2014) but, interestingly, the only previously described specialization of a web-building spider on termite prey was of a related genus, *Chrosiothes*, in which *C. tonala* (Levi 1954) builds horizontal lines above the ground from which to grab and envenomize termites (Eberhard 1991). The delicate *Janula* spiders, with a body size of ~2 mm (slightly smaller than that of their termite prey, Fig. 1A, B), promptly attacked termite soldiers defending the periphery of the breach, usually wrapping multiple prey termites together and webbing them to the outside of the nest before suspending the immobilized termites away from the nest or gallery (Fig. 1B). Spiders with prey invariably attracted kleptoparasitic female adult Ceratopogonidae, some of which fed on the immobilized termites. We describe here the details of these novel associations.

We made diurnal observations of termites, spiders and flies at four nests of *Nasutitermes ephratae* between May 4–9, 2009, in a small area of wet forest adjacent to the main buildings of the Estación Científica Yasuní of the Pontificia Universidad Católica del Ecuador (250m, 0°40′41″S 76°23′48″W). No spiders were seen at several nearby nests of arboreal termites of other species. The subject *Nasutitermes ephratae* nests (Fig. 1C) were located more or less at eye level, and when the thin, paper-like shells were ruptured (poked with a stick), numerous soldier termites immediately appeared at the point of damage; spiders appeared shortly thereafter. We noticed no silk lines attached to the nest prior to manipulation. Behavior was documented with both still photography and video, and voucher specimens were collected. Newly killed termites were set out near two of the four nests to see if the spiders and/or ceratopogonids were attracted to immobilized termites outside the spider's caches. We aspirated Ceratopogonidae from around spiders and their termite prey, stored them in 70% alcohol, and later slide mounted the specimens using the method described by Borkent & Spinelli (2007).

Although we saw no *Janula* spiders on or near intact nests, 1–5 spiders appeared within five minutes of damaging each nest. Prey soldier termites were picked off the periphery of the breach by spiders clinging to the outer nest surface adjacent to the breach. The spiders moved to nearby termites on the nest surface, grabbed them with their legs, and webbed them to the nest surface. Multiple termites were bitten while on or near the nest or gallery prior to being webbed together. Spiders bundled one or more (Fig. 1D) termites into a ball. They then secured silken strands to a nearby leaf or branch, attached a strand to the now immobile bundle of termites, and swung out from the nest with their prey. They proceeded to feed slowly on the termite soldiers where they hung in space away from the termite nest. Some spiders returned to the termite nest to capture further prey, swinging out with prey and adding them to the initial bundle.

Ceratopogonid flies were observed on or around the spider's termite bundles at each of the four observed nests. Each bundle eventually attracted 1–4 flies that hovered nearby (Fig. 1E, F), darted in and out, and briefly (from a few seconds to a few minutes) fed on the wrapped termites. Still photographs clearly show the fly mouthparts inserted into the prey (Fig. 1D). Attending spiders were clearly agitated by the flies, waving their legs at the flies in apparent defense (Fig. 1F). Although no successful attack on a fly was observed, some of the termite bundles included dead ceratopogonids (Fig. 1D), suggesting that kleptoparasitism of *Janula* carries some risk. Flies appeared soon after the termite bundles were hung and persisted throughout the period of observation (up to 24 hours on one bundle). The flies sometimes landed nearby for short periods, but showed no interest in the dead termites laid out nearby. No ceratopogonids were seen on or around the Reduviidae feeding on the termites at the same nests. The ten flies collected on or near the wrapped termites were of four species of blood-feeding Ceratopogonidae in two genera (see below for details of the fly taxa).

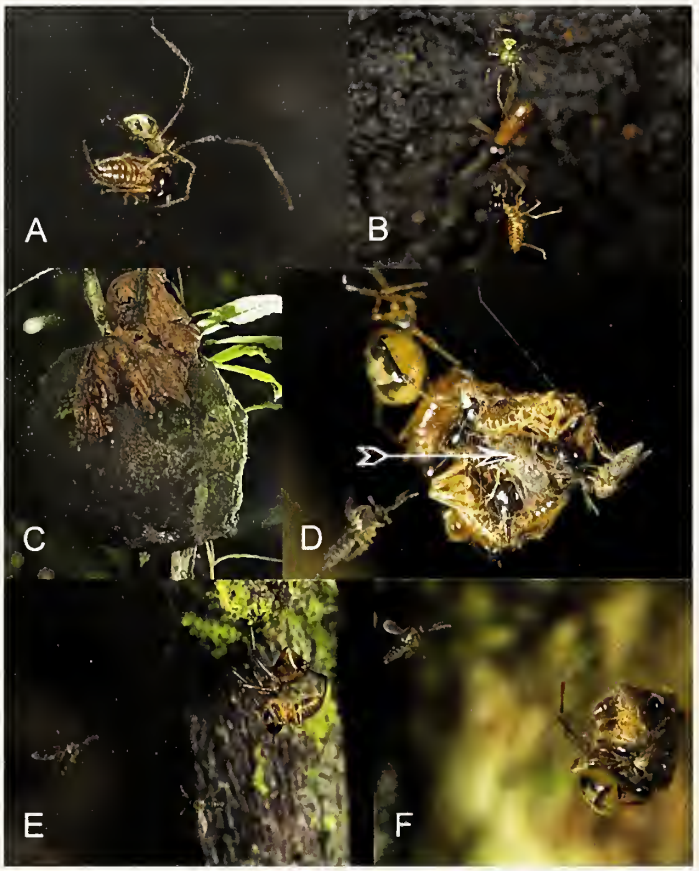

Figure 1.—A) *Janula* sp. with a single soldier of *Nasutitermes ephratae*; B) *Janula* sp. swinging out from a *Nasutitermes ephratae* nest with a single termite (lower termite in the photo) in tow; C) *Nasutitermes ephratae* nest with a breach in the outer wall; D) Female *Forcipomyia* sp. feeding on immobilized termites; the bundle of termites includes at least one dead *Forcipomyia* (arrow); E) *Janula* sp., with a single prey *Nasutitermes ephratae* soldier, fending off two kleptoparasitic female *Forcipomyia* sp.; F) *Janula* sp. with hanging ball of immobilized termites; a female *Forcipomyia* hovers nearby.

Repeated observations of consistent modes of attack, transport and storage of prey by *Janula* spiders on four *Nasutitermes ephratae* nests suggest that termites are an important food source for this spider species. Given these observations and the relative rarity of termitophagy in spiders (Pekár and Toft 2014), we hypothesize that the spider is a specialized termite raider. Spiders were found on all four *N. ephratae* nests observed but were not found on either intact or ruptured nests of other, more abundant termites in the same area, further suggesting that it is a specialized raider of *Nasutitermes ephratae* nests. Additional experimental studies are needed to test these intriguing hypotheses.

Several families of flies are known to be kleptoparasites on spider prey (Sivinski et al. 1999) and are often attracted in groups of numerous individuals that may consist of multiple species (Sivinski et al. 1999; Kuntner & Agnarsson 2010). The frequent appearance of the ceratopogonid flies at each colony, but only on bundled termites, suggested a specialized kleptoparasitic relationship. This relationship is remarkable in that four species of fly were involved and that biting midge and spider associations are rare (Sivinski et al. 1999).

No other *Janula* species is known to attack termites, but one other theridiid species (*Chrosiothes tonala*) has been described as preying on foraging workers and associated soldiers of a subterranean termite, *Tenuirostritermes briciae* (Snyder), in Mexico (Eberhard 1991). This species also immobilizes multiple individuals, transporting them before hanging them under leaves or stems, often in large masses of 20 or more individuals. *Chrosiothes tonala,* however, has an otherwise very different attack strategy, dropping down on foraging termites on the surface of the ground from above rather than attacking soldiers at a nest breach as in the species considered here. Most theridiid spiders rely on webs to stop and entangle prey, facilitating their capture (Agnarsson 2004). However, both *Janula* and *Chrosiothes* belong to the subfamily Spintharinae (Agnarsson & Veve 2015). Most spintharines appear to be specialists on pedestrian prey, and some physically subdue prey rather than relying on webs. Prey capture strategies are known for only very few spintharines and the observations discussed here suggest that further studies may uncover diverse and unusual prey capture strategies within this subfamily.

Females of many species of the biting midge subfamily Forcipomyiinae feed on insects much larger than themselves, including such hosts as caterpillars, phasmids, wings of Odonata and Lepidoptera, blister beetles and more (Borkent & Spinelli 2007). There are very few observations of Ceratopogonidae female adults feeding on spider prey other than the records of *Atrichopogon* in Downes & Smith (1969). Three unidentified *Forcipomyia* were observed by W. Eberhard (pers. comm.) on a spider web on Isla del Coco, Costa Rica but it was uncertain if they were feeding. One species of *Forcipomyia, F. araneivora* Clastrier & Legrand from Guinea, has been observed feeding directly on a spider (Clastrier & Legrand 1991), the only ceratopogonid known to do so.

The subfamily includes two genera, *Forcipomyia* Meigen and *Atrichopogon* Kieffer. The 10 specimens found here all have biting mouthparts and were collected pursuing the spiders and their captured termites. Of these, a single female of *Atrichopogon* (*Lophomyidium*) sp. resembles some undescribed Costa Rican species that can only be distinguished on the basis of male specimens (Borkent & Picado 2004). The genus *Atrichopogon* is large, with 521 described species worldwide (Borkent 2014). However, there are records of feeding for only nine other described species on either true or false blister beetles (Meloidae, Oedemeridae) or the wing of a Lepidoptera. Downes & Smith (1969) observed unidentified *Atrichopogon* feeding on dead insects in a spider web, the only other observation of this genus besides ours of an association with spiders. Three species of *Forcipomyia* were also sampled. Two of these are in the subgenus *F.* (*Warmkea* Saunders) and are the first records of biting in that group. Six specimens were of *F. galindoi* Wirth and Soria, a species more broadly distributed in the Neotropical Region (Borkent & Spinelli 2007). Two specimens were *F. terrestris* Saunders, a species previously known only from Trinidad (Borkent & Spinelli 2007). One specimen of *Forcipomyia* (*Euprojoannisia* Brèthes) could not be identified to species. All ceratopogonids photographed feeding on the bundled termites were *Forcipomyia* Meigen.

The observations reported here document a previously unknown prey capture strategy of a theridiid spider and confirm persistent kleptoparasitism by ceratopogonid flies attracted to the immobilized termite prey. Given the rarity of ceratopogonids feeding on spider prey, it was unexpected to discover four ceratopogonid species associated with this specialized Ecuadorian *Janula* species. In the light of this finding it would be worthwhile to determine whether the flies feeding from the spider-bundled termites are the same as those seen flying around the spider and prey. This biological system warrants further study to more fully document the natural history of this remarkable termite-hunting spider and its relationship with multiple species of biting midges.

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SHORT COMMUNICATION

Influence of ambient temperature on efficacy of signals produced by female *Schizocosa ocreata* (Hentz, 1844) (Araneae: Lycosidae)

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Abstract. The ambient temperature of an environment has potential to influence many aspects of the behavior and physiology of small-bodied ectotherms, including brush-legged wolf spiders *Schizocosa ocreata* (Hentz, 1844) (Araneae: Lycosidae). Temperature varies significantly, and often unpredictably, in their habitat throughout the spring breeding season, and is known to influence male *Schizocosa* courtship behavior. Currently unknown is what effect fluctuations in ambient temperature alone might have on critical, non-behavioral sexual signals such as female silk and chemical cues. We collected cues from mature, virgin females and subjected each sample to one of three thermal treatments (40°C, 20°C, or -12°C), at constant humidity. We presented treated female cues to mature males and recorded male response across treatment types as a behavioral indicator of signal degradation. There were no significant differences across treatments in the frequency or duration of male behaviors, including critical courtship and exploratory behaviors. Our results suggest that thermally induced degradation of female sexual signals is negligible for this species and likely has little or no influence on male behavior.

Keywords: Wolf spiders, chemical cues, silk, signal degradation

The ambient temperature of an environment has the potential to influence many aspects of the behavior and physiology of small ectotherms. In wolf spiders (Lycosidae), ambient thermal variation has been shown to influence courtship vigor, copulation duration, and reproductive output (Davis 1989; Jiao et al. 2009; Chen et al. 2010). *Schizocosa ocreata* (Hentz, 1844) is a common wolf spider found in the leaf litter of eastern deciduous forests of North America where temperatures vary spatially, diurnally, and seasonally across the spring breeding period (April–June) (Cady 1983; Augspurger 2009, 2013; Roberts unpubl.). When moving through their habitat, female *S. ocreata* deposit silk and chemical cues that provide distinguishing information to males such as species identity, age, and mating status (Roberts & Uetz 2004a,b, 2005). Males of this species respond to appropriate female cues with active courtship and exploratory behavior (Stratton & Uetz 1981; Roberts & Uetz 2004a), and spend a significant amount of time moving through the leaf litter actively seeking hidden females (Cady 1983).

Thermal fluctuations in the environment influence *Schizocosa* male courtship behaviors, where courtship vigor is positively correlated with temperature (Davis 1989). Currently unknown, however, is how ambient temperature may affect other aspects of sexual signaling in this genus, especially with regard to female signals that include silk and/or chemical cues. The possibility exists that some of the variation in temperature-affected behavior by male *Schizocosa rovneri* (Uetz & Dondale 1979) noted by Davis (1989) could be explained by thermal influences on silk-bound female chemicals, the physical structure of the silk, or some interaction of the two. In a study of *Schizocosa malitiosa* (Tullgren 1905), Baruffaldi et al. (2010) found, using male courtship and exploratory responses, that male response declined quickly when female silk and chemical cues were exposed to natural environmental conditions. They concluded that humidity and/or dew was the likely cause of this induced female signal degradation, though they suggested that other untested environmental factors such as sun exposure or ambient temperature could be contributing factors (Baruffaldi et al. 2010). We concur with their findings and sought to specifically rule out the effect of thermal environment on signal degradation. We explored the possibility that ambient thermal environment alone could lead to signal degradation by exposing female *Schizocosa ocreata* silk and chemical cues to thermal extremes and then presenting the treated samples to males. Because males within the genus *Schizocosa* respond reliably to virgin adult female chemical and silk cues with active courtship if such cues are present (Roberts & Uetz 2004a; Roberts & Uetz 2005; Stratton 2005), male behavioral response provides a reliable biological assay of signal quality.

In September and October of 2011, we collected immature spiders at The Dawes Arboretum, Newark, Ohio, USA (39.973863°N, 82.40128°W), and returned them to the lab to be raised to maturity in individual plastic containers (500 ml, round). We fed spiders 2–3 cricket nymphs (*Acheta domestica*) twice weekly, and provided *ad libitum* access to water via moistened, coconut fiber substrate. All individuals used in experiments were between one and four weeks of maturity (post final molt) in order to maximize male response (Roberts & Uetz 2005), and we randomly selected mature female (n = 21) and male (n = 42) *S. ocreata* from the appropriately aged lab population. We modified the methods of Roberts & Uetz (2005) to standardize collection of silk and chemical cues from females. Specifically, we placed each female on a clean disk of filter paper (Fisherbrand, 11 cm dia. round) within a ring of PVC (polyvinyl chloride, 10 cm dia., 5 cm high) and then gently prodded the female with a horse-hair brush until she made 50 circuits around the inner circumference of the ring. Because females naturally deposit dragline silk and chemical cues as they move through the environment (Uetz & Roberts 2002; Foelix 2011), this method prevented females from settling in any one location for an extended period, and provided us with relatively consistent and uniformly distributed cues on each filter paper disk.

At the end of the collection period, we returned each female to her individual container and placed the cue samples in air-tight/moisture-tight plastic bags. Isolating cue samples at constant humidity prior to thermal treatment protected the silk in the samples from excessive

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hydration or desiccation (following cooling or heating, respectively), which are well known to alter mechanical properties of spider dragline silk (e.g., supercontraction, conformational changes). (Guan et al. 2011, 2013), and which may deactivate chemical cues (Baruffaldi et al. 2010). In our behavioral assay (described below), males make direct contact with silk in the cue sample. The sensitivity of males to conformational changes in female silk is unknown and thus we attempted to limit such changes by keeping the cue samples isolated. Prepared samples were always used within 24 hrs of collection. Using a one-way ANOVA design, we randomly assigned each isolated sample to one of three temperature treatments; Hot (40°C), Control (20°C), or Cold (-12°C). We selected maximum and minimum temperature treatments somewhat outside the range of normal variation at the field site during the breeding season to increase the likelihood of inducing and detecting thermal degradation or disruption of the signals (Roberts unpubl.). We held each sample at the appropriate treatment temperature for 60 minutes.

Following the thermal treatment, we kept cues sealed in sample bags, placed them on the lab bench in a single layer, and using results of preliminary experiments as a guideline, allowed them 15 minutes to return to ambient temperature (approx. 20°C) prior to use in a behavioral assay trial. We used an infrared thermometer (Raytek® model: RAYST60XBUS) held 10 cm from the surface of the sample to confirm temperature of the sample prior to use. For each behavioral trial, we removed a sample from a sample bag, cut the filter paper disk in half, and then used each half of a given sample with a different male to control for variation among females (Roberts & Uetz 2005). To start a trial, we cut each filter paper segment in half again (for better fit) and placed both sections into the bottom of a clear plastic box (10 cm x 10 cm x 25 cm). We gently deposited a male onto the sample from above and video recorded the resulting behavior during the five-minute trial. We cleaned the plastic boxes and scissors with 70% ethanol and a clean Kimwipe© between trials, then allowed them to air dry, removing all traces of silk and chemical cues. We scored each recorded trial according to a published ethogram of male *S. ocreata* behaviors (Roberts & Uetz 2004a) using JWatcher (vers 1.0). All behaviors were analyzed for differences in the total number of bouts (frequency over trial) and total duration (total time performing behavior over trial) across treatments using JMP (vers 9, SAS Institute). To meet the assumptions of ANOVA, we log transformed total duration data and square root transformed frequency data (Martin & Bateson 2007). We excluded a single trial from the "Cold" treatment due to a filming error (caused by a power outage during filming) resulting in the following final sample sizes: Cold (n = 13), Control (n = 14); and Hot (n = 14).

We found no significant negative influence of thermal treatment on the total number of behavioral bouts or total duration of behavior of males for any of the recorded behaviors, including critical courtship and exploratory behaviors (Table 1, Fig. 1). All behaviors were performed at rates and durations consistent with responses to untreated female chemical and silk cues found in earlier studies (Roberts & Uetz 2004a, 2005). These results indicate relative thermal stability within the range of natural thermal variation for the cues involved. Any thermally induced signal degradation that may have occurred must have been below male detection thresholds, because the signal remaining after treatment was sufficient to induce normal behavioral responses.

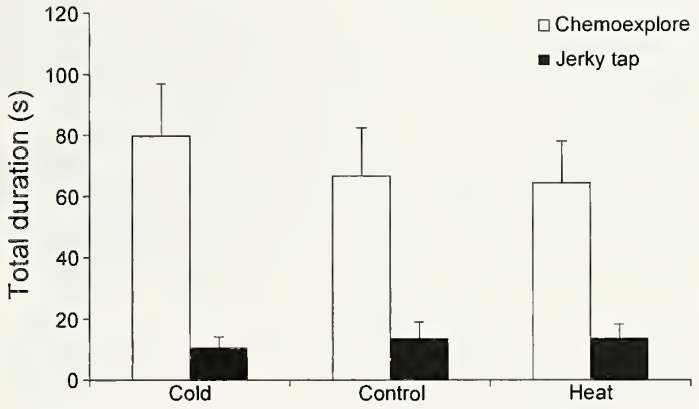

Figure 1.—Mean total duration of bouts (+SE) of Chemoexplore and Jerky Tap behaviors performed in response to female silk and chemical cues across thermal treatment categories.

Thermal treatment of the cue samples in our experiment does not appear to have fundamentally changed the nature of the cues themselves, or the underlying information content. This provides further support for Davis (1989), who demonstrated that thermal environment significantly influenced male courtship behavior in *Schizocosa rovneri*. Male response by temperature was almost certainly due to the physiological effects of ambient temperature on the males (Davis 1989), and not due to some change in quality or information content of the female cues. The apparent thermal stability of signals associated with female *Schizocosa* silk also lends support to the findings of Baruffaldi et al. (2010), who demonstrated a decline in male response to female cues that had been exposed to the natural environment. Variation in ambient temperature of the natural environment probably did not contribute to the inactivation of female signals that led to declining male courtship response over time (Baruffaldi et al. 2010), except in its capacity to contribute to atmospheric condensation/dew formation within the microhabitat. Thermal stability of female cues further confirms that the active signaling chemicals are high molecular weight compounds deposited with silk, as has been previously indicated for *Schizocosa* (Roberts & Uetz 2004a; Baruffaldi et al. 2010), and helps guide future studies of the specific chemical nature of substrate-bound signal compounds in these wolf spiders.

Table 1.—ANOVA results for behaviors of male *Schizocosa ocreata* in response to female cues. Significance indicated at Bonferroni adjusted α=0.007 (*ns* = not significant). Ethogram adapted from Roberts & Uetz (2004a). Jerky tap is active courtship behavior in males and Chemoexplore is active exploratory behavior.

	Total number				Total duration			
Behavior	F	df	*P*		F	df	*P*	
Jerky tap	0.281	2,38	0.757	*ns*	0.096	2,38	0.909	*ns*
Tap	1.671	2,38	0.202	*ns*	1.022	2,38	0.370	*ns*
Leg raise	0.723	2,38	0.492	*ns*	0.646	2,38	0.530	*ns*
Chemoexplore	0.276	2,38	0.760	*ns*	0.190	2,38	0.828	*ns*
Grooming	1.175	2,38	0.320	*ns*	0.715	2,38	0.496	*ns*
Locomotion	2.098	2,38	0.137	*ns*	1.127	2,38	0.335	*ns*
Stationary	1.758	2,38	0.186	*ns*	0.884	2,38	0.422	*ns*

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